Winfried Henke
Ian Tattersall
Editors

Handbook of Paleoanthropology

Second Edition

SpringerReference

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With 392 Figures and 74 Tables

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Editors
Winfried Henke
Institut für Anthropologie
Johannes Gutenberg-Universität Mainz
Mainz, Germany

Ian Tattersall
Division of Anthropology
American Museum of Natural History
New York, NY, USA

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Preface to the Second Edition

Knowledge is advancing rapidly in all areas of science, and the science of paleoanthropology is certainly no exception. Yet, it was still a surprise, a mere 4 years after the *Handbook of Paleoanthropology* first appeared, to hear from Mrs. Susanne Friedrichsen, senior editor at Springer and our editor for the first edition, that she and Mrs. Hanna Hensler-Fritton, editorial director of life sciences and biomedicine at Springer and successor to Dr. Dieter Czeschlik, who had initiated and enthusiastically supported the project, were already thinking about an updated and possibly even enlarged new edition.

Naturally enough, we were a little hesitant. Of course, we were happy to hear that the handbook had been sufficiently successful for the publisher to contemplate a new edition. But, on the other hand, both of us had recently retired and were looking forward to the tranquil pursuit of pet projects that had previously had to be put on the back burner. What's more, we knew from experience how huge a commitment would be involved. And then, there was the indefatigable multivolume encyclopedist Bernard Wood's comment in a review of our first edition: "The timelessness of the research problems means that from time to time folks will always want to take stock of what progress, if any, we have made toward solving these problems, but I fancy it will be brave ones who try to do this in the future in the form of three printed volumes. My prediction is that the *Handbook of Paleoanthropology* will suffer the same fate as the Neanderthals" (*Evolutionary Anthropology* 17: 119–122, 2008).

Should we be brave, and did we even want to be? During a meeting in Heidelberg, Germany, one of us (WH) was introduced to the new workflow system SpringerReference.com by Mrs. Hensler-Fritton and Mrs. Friedrichsen, who expressed boundless and infectious enthusiasm for the new facility. We learned that the handbook would be available online as well as in hard copy and that the system was sufficiently flexible for authors to make their own updates directly online. With this option for continuous updating, the attractiveness of the project increased.

So in the end, we decided to leave the decision to our contributors. If they were ready to proceed and to update and expand their contributions, then we were prepared to go ahead and edit a new edition. Quite frankly, we had no idea how they would react. As a first step in assessing the willingness of our contributors to proceed, we wrote in January 2012 to all of our original authors inviting them to cooperate once more and telling them of the new game plan. The feedback was overwhelming. Fewer than one-tenth of our 67 contributors declined, though many, predictably enough, requested extended deadlines. And everyone we subsequently approached agreed to write replacement chapters. With such a response, we had no choice but to press ahead. In the process, we added new material with the benefit of the input, especially from reviews, that the first edition had generated.

By Easter 2014, 76 articles had been submitted, and we hope that the thoroughly revised, enlarged, and updated second edition adequately reflects the many changes that have impacted the sciences of human evolution since the first edition appeared. We are pleased to make it available to all those students and professionals who are interested in paleoanthropology defined in its broadest sense and in its principles, methods, and approaches.

The concept of the first edition has not been changed, and, as then, we have not tried to impose any uniformity of viewpoint on our authors. Indeed, we have welcomed heterogeneity of opinion and have had the luxury of giving authors sufficient space to lay out all the evidence they consider relevant to allow every reader to reach his or her own conclusions. In addition, the online version allows the inclusion of unlimited colored figures: a welcome improvement and an aesthetic delight especially in those contributions that discuss glorious fossils and marvellous artifacts. As we expect most readers to use the easily searchable SpringerReference.com version and not the hardcover publication, we have reduced the basic index to keywords indicated by the authors. For the same reason, the taxonomic index is restricted to genera and species only.

That we are in the happy position of writing this preface exactly 3 years after we began negotiations on this second revised and enlarged edition is due to the contributors who worked so diligently on the updates of their chapters (only four survive intact from the first edition). Some topics needed more input than others, but we thank all authors equally. It has been a pleasure working with them. We additionally extend special thanks to those colleagues who took on the task of writing (with an entirely free hand) replacement versions of old chapters and chapters on themes that were not addressed in the original edition. It has been great working with you all.

On the editorial side, we are especially grateful to Mrs. Hanna Hensler-Fritton and Mrs. Susanne Friedrichsen, already mentioned, whose enthusiastic support for the project and for integrating the handbook in the live reference system (Springer-Reference.com) was crucial for its realization. During the first stage of the project, the coaching of the authors in its technicalities was done with patience and commitment by Ms. Swati Sharma, previously associate editor, MRW, Springer, New Delhi. When Ms. Sharma's functions were handed over to Ms. Audrey Wong, associate editor, MRW, Springer Science+Business Media, Singapore, at the end of 2012, we were again in highly professional hands. The continuous dialogue with Ms. Wong and later on with Ms. Meetu Lall and subsequently Ms. Sunali Mull greatly facilitated the shepherding of the submissions through the initial production process. We are grateful to all of these dedicated people. At SPI Technologies, we also thank Mrs. Christine Bartels for her extraordinary copyediting expertise and Ms. Anitha Rajasekaran, Project Manager, SPi Technologies India Private Ltd, for deft assistance in the later stages of the production process.

January 2015

Winfried Henke
Mainz, Germany

Ian Tattersall
New York City, USA

Preface to Volume 1, Second Edition

Principles, Methods, and Approaches

Although in the 7 years since the appearance of the first edition of the *Handbook of Paleoanthropology* there have been no paradigmatic changes in paleoanthropological thinking, the field has been energized by numerous theoretical developments (e.g., epigenetics, symbolism), methodological innovations (e.g., virtual anthropology, paleogenetics), and highly innovative collaborative approaches to paleoanthropological research (e.g., NESPOS, EVAN). There have additionally been exciting new paleogenetic (e.g., the Neanderthal genome, Denisovans), fossil (e.g., *Australopithecus sediba*) and artifactual (e.g., Swabian Venus of Hohle Fels) findings that provide more than enough reason for an update. This second edition has also given us the chance to integrate additional contributions too (e.g., on Charles Darwin, paleoanthropology, and the modern synthesis; the relationship of paleoanthropology and genetics; the evolution of speech and language; virtual anthropology and biomechanics; the investigation of human fossils using medical technologies; and facial reconstruction in paleoanthropology).

2009 marked the bicentennial of Charles Darwin's birth and the 150th anniversary of his seminal *On the Origins of Species by Means of Natural Selection* that gave biology its most important unifying concept. This double anniversary was celebrated by innumerable events and gave rise to intense biographical research and reflection on the state of evolutionary biology. In the opening chapter, **Winfried Henke** tries to integrate some of this introspection in a detailed update of his "Historical Overview of Paleoanthropological Research." He demonstrates that a historiographical glance backward, even as we move forward, will be helpful in making us more critical about the reliability and validity of our theoretical concepts, methodological approaches, and empirical bases. It is obvious that the change from monocausal explanations to a more complex and multifaceted thinking (e.g., biomechanical and energetic aspects as well as such things as ecological and nutritional prerequisites) has led to better explanations of the process by which we became human – but he warns that we still should not expect too much of models! Many problems remain unsolved and pose challenges for future research.

As a belated tribute to Darwin's double anniversary, we asked **Franz M. Wuketits**, evolutionary biologist and philosopher of science, to focus on the role paleoanthropology played in Charles Darwin's views of evolution and later on in the formation of the synthetic theory or modern synthesis. His essay "Charles Darwin, Paleoanthropology, and the Modern Synthesis" is a critical review of Darwin's concepts of human evolution as developed in *The Descent of Man*. He analyzes the role of Darwin's thoughts in establishing the synthetic theory in the 1930s and 1940s, although only later were most leading proponents of this theory explicitly concerned with paleoanthropological issues. His chapter also recalls some historical examples showing how paleoanthropologists have sometimes been misled by ideology (*Weltanschauungsfragen*). Wuketits brings methodological issues to the fore and rightly emphasizes that these matters deeply affect the status of a discipline that is of crucial importance for understanding the human condition, past and present. **Philippe Huneman's** contribution on "Evolutionary Theory in Philosophical Focus" has been wholly rewritten. This critical essay from the perspective of a philosopher is now more accessible to those who are unfamiliar with philosophical methods. The survey focuses on the philosophical problems raised by two of Darwin's claims: the existence of a tree of life and the explanatory power of natural selection. Huneman's overview illustrates that evolutionary theory is replete with theoretical problems over such basic concepts as selection, fitness, and adaptation. His perspective that "those problems are at the same time philosophical since they involve conceptual matters that imply epistemological and metaphysical options" is a challenge to all those who wish to escape the generally reductionist views of biology, and it may have relevance to such long-standing puzzles as the origin of language, maternal attachment, morality, and cultural evolution. **Peter Menke** has produced a slightly enlarged update of his contribution "The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology" in which he explains via the example of the cranial base how ontogeny can help illuminate the processes of human evolution. **Michael Ohl's** excellent contribution on "Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms," commended as "a jewel" by a reviewer of the first edition, has remained unchanged. **Colin Groves** has contributed a minor update to his chapter on species and speciation (previously in Volume 3). **Kaila Folinsbee** and coauthors' contribution on "Quantitative Approaches to Phylogenetics" has been expanded by the integration of numerous new references, while **Oliver Rieppel's** article on "Homology: A Philosophical and Biological Perspective" has also retained its structure from the first edition.

The last few decades have seen ongoing developments and methodological progress in the field of chronometric dating, and we are very grateful to **Daniel Richter**, who took over the task of extensively updating **Günther Wagner's** "Chronometric Methods in Paleoanthropology." This comprehensive contribution introduces the reader to the principles of radiometric dating and to the most frequently applied dating methods such as argon/–argon, uranium series, luminescence, electron spin resonance, and radiocarbon. Their potential for paleoanthropology is illustrated using various examples covering the entire period since hominins first entered the scene several million years ago. Of special interest is a new section on the cosmogenic ^{26}Al/^{10}Be technique successfully applied at such sites as Sterkfontein, Atapuerca/Sima del Elefante, and the Lower Cave at Zhoukoudian. This article impressively illustrates how paleoanthropological knowledge and concepts have benefited from these methodological advances. **Walter Etter** provides a broad view of "Patterns of Diversification and Extinction," and his meticulously rewritten history of life on Earth reaches back to the beginning of organic life. This places human evolution in an extremely broad perspective. Etter points out "that each extinction event had its own signature, and no common cause has been found." The Phanerozoic has seen 5 major and more than 15 smaller mass extinctions that disrupted the diversification of life and sometimes drastically altered the path of evolution, and Etter expresses concern "that we are currently entering a 'Sixth' major extinction, caused by human impact on nature."

Taphonomic processes lead to a stepwise loss of information about formerly living organisms, so understanding the transition of organic remains from the biosphere to the lithosphere is essential. **Gisela Grupe's** update coauthored by **Michaela Harbeck** on "Taphonomic and Diagenetic Processes" therefore gives a comprehensive and up-to-date overview of the successive steps of necrology, biostratinomy, burial, and diagenesis. The revised chapter contains additional sections dealing with mineral changes, e.g., the recrystallization and/or the preferential loss of smaller crystallites in the course of mineral dissolution leading to an increase in bone crystallinity, a most fundamental aspect of bone diagenesis. She further covers the preservation of biomolecules, an increasingly important topic. Stable light isotopes allow us to detect linkages between hominin evolution and environmental changes, and **Julia Lee-Thorp** and **Matt Sponheimer's** updated "Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction" integrates many recent studies. The authors convincingly demonstrate that "carbon isotope ratios of pedogenic carbonates and faunal enamel have pushed back the emergence of C_4 grasses, and thus more open environments, to ca. 9 Ma," and as a further remarkable result, they cite isotopic evidence from East and South Africa that "suggests a significant change to more open, grassy ecosystems ca. 1.8 Ma, broadly concordant with the emergence of *Homo ergaster*." These and many other results demonstrate the great importance of isotopic approaches to understanding paleoenvironments. **John Rowan** and **Kaye E. Reed** have provided a new contribution on "The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments." Their concisely written overview of various paleoecological methods summarizes recent results on the paleoecology of hominins from the late Miocene to the early Pleistocene, ~2.0 Ma. For habitat reconstruction bases on fauna, the use of taxon-free methods (e.g., enamel isotopes) is preferred over taxon-based methods (e.g., tribal relative abundance) because the latter involves considerable assumptions, e.g., sites containing *Australopithecus* are often reconstructed as "mosaics." The authors note that this could be due to time averaging or depositional processes or might actually represent various habitats across the landscape.

There is no doubt that Africa is the "cradle of human origins," and it is highly likely that many fossils still await unearthing. **Ottmar Kullmer** asserts in his contribution on the "Geological Background of Hominid Sites in Africa" that "the types of sediments and the geological contexts likely to yield hominid fossils are known. We just have to look for the right deposits." His contribution adds recent literature and gives us a comprehensive overview of the topic. Kullmer advises all "fossil-hunters" to look not only at those sites and regions that yielded hominin fossils in the past but encourages them to "discover new fossiliferous localities in smaller-scaled graben and basin structures at places in central, western or southwestern Africa." As an experienced field paleontologist, he is convinced that ". . .it is just a matter of time until the first early hominid is reported from the other side of the African continent." Let us hope he is right! Soils are "products of environmental factors such as climate, vegetation, topographic setting, parent material, and time for formation," so that "paleosols, or fossil soils," give us the chance to reconstruct changing environments in the past. **Gregory Retallack's** contribution on "Paleosols" does not support the traditional narrative of human evolution in a single transition from primeval forest to dry climate and open grassland. Research on paleosols indicates climatic oscillations between wet and dry and alternating expansion of woodland and grassland since at least 18 Ma (million years ago). Since paleosols do not reproduce well in black and white, it is a great improvement to see the figures in color in the online version. **John A. Van Couvering's** new article on "Quaternary Geology and Paleoenvironments" characterizes the late Neogene in environmental terms both globally and as it applies to African and Eurasian environments. Topics include the chronostratigraphic divisions of the Quaternary, the cause and timing of the climatic cycles, the development of grasslands and deserts, sea-level changes and their effects on human migration, and the apparent synchronicity of hominin evolutionary steps and major climate shifts. Van Couvering emphasizes that "the appearance of *Homo* just as climate changes became significantly more extreme with the beginning of the Quaternary cannot be a meaningless coincidence" and avers that ". . .if we accept that natural selection is driven primarily by environmental change, we cannot avoid a very strange and simple conclusion: that the breakthrough into sentience that makes us able to read and write these words about the Quaternary would not exist, but for the existence of the Quaternary itself." **Klaus-Dieter Jäger's** contribution on "Quaternary Deposits and Paleosites" has been updated and deals mainly with European paleosites of the Pleistocene and Holocene epochs. Though the Quaternary, characterized by a series of significant long- and short-term climatic fluctuations, is comparatively short, it is of special paleoanthropological interest because it saw the origin and expansion of the genus *Homo* and the rise of anatomically modern *Homo sapiens*. **Thorolf Hardt** has slightly updated his coauthored contribution on "Paleoecology: An Adequate Window on the Past?" and we hope that the view through the "window" is a bit clearer now. Sadly, **Alan Turner**, world authority on the evolution of mammalian faunas of Africa and Europe, passed away in January 2012. But his coauthor, **Hannah O'Regan**, took on the task of updating their joint and content-rich overview of "Zoogeography: Primate and Early Hominin Distribution and Migration Patterns." Putting paleoanthropology into paleoecological focus, the new version integrates essential new literature on this challenging issue. Even more difficult is "The Paleodemography of Extinct Hominin Populations" treated by **Alan Mann** and **Janet Monge**. As demographic structures are both the outcome of evolutionary processes operating on groups of individuals and the basis on which future evolutionary forces can potentially operate, it is of great interest to have this topic overviewed. However, Mann and Monge find little prospect that our methods and approaches will soon deliver reliable results as “the paleodemography of extinct hominin taxa has not produced a corpus of dependable data, and it remains possible that reasonable population-based demographic parameters from fossil assemblages will remain unattainable into the foreseeable future.” The authors offer some hope, however, in stating that “the use of modeling from archaeological samples holds more promise in an application to the more distant past to capture demographic parameters in long extinct populations in the hominin lineage.” In contrast, isotope research is a highly dynamic and promising field, and the extensive update of **Matt Sponheimer** and **Julia Lee-Thorp’s** contribution on “Hominin Paleodiets: The Contribution of Stable Isotopes” is excellent proof of this. These authors present new data justifying the assumption that the earliest australopiths had nearly pure C_3 diets, whereas later australopiths, living around 2 Ma, show a predominantly C_4 signal. There is further indication that increased masticatory robusticity in the australopiths is associated with greater C_4 consumption; however, given *Paranthropus boisei*’s thick, robust mandibles, low-cusped cheek teeth, and diminutive incisors and canines, the authors believe it improbable that its major C_4 dietary input was meat, and they regard it most parsimonious to ascribe the preponderance of its C_4 signal to the direct consumption of C_4 plant foods like grasses or sedges.

Helmut Hemmer’s article on “Estimation of Basic Life History Data of Fossil Hominids” remains highly useful and informative, whereas **Jonathan Marks** kindly agreed to write a new replacement chapter on “Genetics and Paleoanthropology.” In a dense historical review, he shows that scholars trained in genetics and in anatomy often see evolutionary comparisons in quite different ways, and he demonstrates that their training and the nature of their data often lead geneticists and paleontologists to conceptualize evolution itself differently. Marks elegantly dissects the pros and cons of the various ways in which the two disciplines invoke adaptation, natural selection, and speciation; he points out that morphological and genetic techniques each have their own set of strengths and weaknesses and that there is a need to integrate both into the deciphering of human origins and evolution. **Susanne Hummel** has thoroughly updated her valuable contribution on “Ancient DNA,” which describes the field’s long trajectory from a “highly skeptical accompanied technical approach revealing spectacular results to a sound practice giving access to biological data helping to explain the past.” Her chapter helps us to understand the complexity of the methods involved and their inherent pitfalls and shows how next-generation sequencing gives access to information on entire genomes. While some practitioners believe that new approaches will replace traditional ones completely, it is likely that complete modeling of the past will only be attained in the context of a multifaceted and integrated science.

In the realm of comparative primatology, **Robert W. Sussman** and **Donna Hart’s** update of “Modeling the Past: The Primatological Approach” is an excellent demonstration that reconstructing the evolution of early human behavior from a primatological perspective is much more than mere storytelling. Instead, it is based on the integration of models of several types: first, the referential model (which uses a living species as literal models for particular extinct species); second, the conceptual model (in which a mosaic of morphological or behavioral traits is seen as a broad analogue for reconstructing early hominin species); and finally, the strategic model (which assumes that species in the past were subject to the same fundamental evolutionary laws and ecological forces as species are today). The update of this paper is a highly informative clarification of the authors' exhortation "to use all of the above in what is considered a logical and appropriate manner but always taking into account whether any particular aspect of our model is inconsistent with the evidence presented in the fossil record." "Modeling the Past: The Paleoethnological Approach" by **Paolo Biagi** uses archaeological legacies in an analogous way. His updated contribution considers current evidence (occupation surfaces, structural remains, hunting weapons, fire) from the earliest Paleolithic (Oldowan, Mode 1) in Africa and continues through early sites beyond that continent, maintaining a paleoethnological perspective. **Miriam Haidle's** detailed update of her contribution on "Modeling the Past: Archaeology" impressively demonstrates the recent progress made in a field of research that has undergone a fundamental change from a descriptive-typological discipline to a highly cross-disciplinary one that integrates the humanities and the sciences. Haidle's chapter focuses on the potential explanatory power of archaeology in paleoanthropology, and she draws her conclusions from a diachronic comparison of the typological, technological, functional, contextual, and cognitive facets of archaeological knowledge. This sophisticated approach allows her to answer questions of how prehistoric populations used their cognitive potential and cultural capacities as determined by biological, historical-social, and individual dimensions and limited by environmental constraints.

What makes us unique? **Phillip Lieberman** and **Robert C. McCarthy's** new contribution on "The Evolution of Speech and Language" gives a possible answer to this fundamental question. Their position is that language did not suddenly arise 50,000–100,000 years ago through a mutation that yielded an innate "faculty of language." Further, they are convinced that human speech, language, and cognition derive from anatomy and neural mechanisms that were shaped by Darwinian processes of natural selection but that are shared with other living species. Their contribution ranges from the neuronal anatomy and neurophysiology of the brain to the larynx and the tongue to findings of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and diffusion tensor analysis (DTI) to the linguistic capacities of living nonhuman species, syntax, and semantics and further to the fossil record as well as to paleogenomic findings (FOXP2). In the process, it touches on many controversial issues.

Gabriele Macho's update of her contribution on "General Principles of Evolutionary Morphology" illuminates how fossil hard tissue remains such as bones and teeth provide a wealth of information for evolutionary biologists aiming to reconstruct the phylogenetic histories and functional adaptations of extinct species. She demonstrates that it is not an easy task to decipher the constraints acting on morphology, and describes the limitations we are faced with when interpreting form/function and behavior from morphology. Macho's advice is to carefully choose the appropriate research tools, bearing in mind the limitations specific to each approach, and she recommends a periodic change of perspective by turning around the fundamental questions about the form, function, and behaviors of extinct hominins. "Virtual Anthropology and Biomechanics" is a replacement chapter written by **Gerhard W. Weber,** whose lucid writing and brilliant illustrations convey the author's enthusiasm for his discipline. Weber explains the six main areas of virtual anthropology – digitize, expose, compare, reconstruct, materialize, and share – and conveys the impression of a highly innovative and dynamic subdiscipline of paleoanthropology. The same holds true of "Biomechanics," which allows us to infer certain aspects of function via the study of structural loading. Weber suggests that in spite of the absence of a formal bridge between those two domains of inquiry, there are many areas of overlap and potential cross-fertilization between them. In three linked short chapters, **Michael Schultz** and **Tyede Schmidt-Schultz** describe and illustrate new methods and approaches of investigating human fossils via medical technologies. Their first describes "Paleopathology: Vestiges of Pathological Conditions in Fossil Human Bone" and briefly illustrates the methods and techniques of paleopathology, exemplifying how this discipline can shed valuable light on the reconstruction of the lives of fossil humans by providing information on how afflictions and illnesses affected the daily lives of ancient hominids. This contribution is a plea "to start comparative work in this innovative field, which will allow us to recognize certain tentative aspects which will, in turn, help to significantly enlarge our knowledge on the living conditions of human antecessors." The second, "Microscopic Research on Fossil Human Bone," deals with the methods and techniques of light microscopy, scanning electron microscopy, and the advantages of polarization microscopy. Schultz and Schmidt-Schultz present selected histomorphological findings on fossilized human bones of different taxa (e.g., *Australopithecus*, *Homo erectus*, *Homo neanderthalensis*, and Paleolithic *Homo sapiens*) examined using plain and polarized light. Their special focus is on those morphological features that give clues to the taxonomy and the functional anatomy of early hominids as well as on those which originated during the lifetime of the individual (e.g., individual age at death, physical strain, and diseases). Their third contribution concerns a highly innovative field of biomedical research, namely, the "Investigation on Extracellular Matrix Proteins in Fossil Bone: Facts and Perspectives." For several years now, it has been possible to detect typical extracellular matrix proteins (ECMs), e.g., osteopontin, osteonectin, and osteocalcin, in archaeological bone. Further, it has recently become possible to detect growth factors and hormones (e.g., TGF-β, BMP-2, gonadotropin), bone matrix proteins of the immune system (e.g., IgG, IgA, interleukin), and biomarkers for diseases such as tumor markers (e.g., PSA, PSA/ACT). Finally, typical molecules characteristic of nonspecific infectious diseases (e.g., TNF-α, IFN-γ) and specific infectious diseases (e.g., from *Mycobacterium tuberculosis*, Ag 85) have been isolated from macerated bone, opening the prospect of detecting these ECMs in fossil bone as well. The authors briefly outline the future possibilities of such studies in understanding fossil human species and express their hope of attracting interest in these innovative biochemical methods and in particular in proteomic research among paleoanthropologists

As we said earlier, paleoanthropology is a subject of great public interest and is therefore in large part a media-driven science – as evidenced, for example, by the fact that the covers of *Nature* and *Science* are regularly illustrated not only by hominid fossils but also by facial reconstructions of our extinct relatives. This by itself is sufficient reason to examine the methods by which these images are derived. "Images in Paleoanthropology: Facing Our Ancestors" is **Stefan Schlager** and **Ursula Wittwer-Backofen's** valuable contribution on this topic. Images and visualizations in paleoanthropology have a curiously persuasive power, so we have to ask: What about them is science, and what is fiction? How objective, reliable, and valid are the various methods of reconstructing the faces and bodies of our ancestors? The authors thoroughly decipher the contextual limits and pitfalls of the various approaches available as "on the one hand evolutionary theories and contemporary social ideas influence and shape the view on our ancestors; on the other hand, hominid reconstructions themselves have a high impact on shaping our view." Their chapter gives a critical overview from the earliest facial reconstructions of early humans up to the most recent "virtual" 3D reconstructions. The last entry in this updated and enlarged first volume of the second edition of the *Handbook of Paleoanthropology* is **Jean-Jacques Hublin's** "Prospects and Pitfalls." Hublin discusses the various challenges of access to original fossil materials and to field sites of special interest as well as to metrical and virtual morphological data, biophysical and biochemical data sets, and tissue samples for paleogenomic and other research. Paleoanthropology has never been easy in these respects, and as an experienced field and laboratory researcher, Hublin makes valuable observations and practical suggestions.

Finally, we hope that our 35 updated and newly integrated contributions adequately cover most of the principles, methods, and approaches of paleoanthropology and that they will supply the readers with the basics of this wide-ranging discipline in accessible form. We are deeply grateful to all the contributors for their time and commitment, and any deficiencies remain entirely our own.

January 2015

Winfried Henke
Mainz, Germany

Ian Tattersall
New York City, USA

Preface to Volume 2, Second Edition

Primate Evolution and Human Origins

Human beings' place in nature can only be properly understood against the general background of primate evolution. For this reason, the second volume of the *Handbook of Paleoanthropology* deals with the earliest origins and evolution of our closest mammalian relatives. It features contributions on the wide diversity of fossil and extant nonhuman primates, summarizing the latest comparative primatological research by taking morphological, molecular, ecological, behavioral, and neurological perspectives with the aim of helping reconstruct our deepest primate roots and explaining what makes us human.

Mary T. Silcox and coauthors have updated and expanded their contribution on "Primate Origins and Supraordinal Relationships: Morphological Evidence," showing that during the last decade, much progress has been made in understanding the supraordinal relationships of primates, their ecological niches and diversification, and their pattern of trait acquisition through time. Significant open questions still remain, however, due to wide gaps in the fossil record. **Ryan Raaum** kindly agreed to write a replacement contribution on "Molecular Evidence of Primate Origins and Evolution": an important component of the volume as molecular data have become an important source of evidence on primate evolutionary history especially when primate fossil data are deficient. Raaum reports on current molecular evidence for the branching pattern among the primates, colugos, and tree shrews, touches on the problem of tarsier affinities. He further discusses the insufficiently resolved relationships among *Aotus*, the cebines, and the callitrichines, and in the case of the strepsirhines states that "excluding the early diverging *Daubentonia* lineage, the relationship of the remaining four lemur families almost certainly includes a cheirogaleid-lepilemurid clade but is otherwise poorly resolved by molecular data." He criticizes "absurdly early estimates for the crown primate radiation" and mentions methodological progress in "mostly or completely fossil calibration free divergence date estimation." Another replacement chapter is **Marc Godinot's** "Fossil Record of the Primates from the Paleocene to the Oligocene." His exhaustive article reviews the Paleogene primate fossil record according to higher systematic categories. Godinot masterfully overviews the radiations and Eocene dispersal pattern of the fossil strepsirhines in North America (Notharctinae) and

Europe (Cercamoniinae, Adapinae), tries to disentangle the role of the poorly understood diversification of the Asian Sivaladapidae, and deciphers the African origin of living Lemuriformes in the late Eocene. Further, he documents the Eocene florescence of Omomyiformes in North America (Anaptomorphinae, Omomyinae) and in Europe (Microchoeridae) and discusses the role of Asian middle Eocene Tarsiidae relative to the character-based definition of Haplorhini. His journey through the Eocene-Oligocene primate taxa begins with the enigmatic Eocene South-Asian Amphipithecidae and ends by characterizing the Anthropoidea, or Simiiformes, documented in the late Eocene and Oligocene of Africa (Parapithecidae, Proteopithecidae, Oligopithecidae, Propliopithecidae). Godinot's contribution ranges over about 20 million years of primate evolution and includes many other relevant aspects of anthropoid origins including locomotion, diet, vision and other sensory capacities, brain evolution, and social structure via sexual dimorphism. Hominoids, or taxa identified as hominoids, are known from much of Africa, Asia, and Europe following the Late Oligocene. The earliest such taxa from Africa resemble extant hominoids but share with them mainly primitive characters. Middle and late Miocene taxa are clearly hominoids, and by the end of the middle Miocene, most can be attributed to either the pongine (*Pongo*) or hominine (African ape and human) clade. Interestingly, there is no definitive fossil record of the hylobatid clade (gibbons and siamangs) though some candidates have been proposed. Miocene hominoids experienced a series of dispersals between Africa, Europe, and Asia that mirror those of many other contemporaneous land mammals. These intercontinental movements were made possible by the appearance of land bridges, changes in regional and global climatic conditions, and evolutionary innovations. Most of the attributes that define the hominids evolved in the expansive subtropical zone that was much of Eurasia. Hominines and pongines diverged from each other in Eurasia, and the final Miocene dispersal brought the hominine clade to Africa and the pongine clade to Southeast Asia. Having moved south with the retreating subtropics, hominines and pongines finally diverged *in situ* into their individual extant lineages.

David R. Begun's carefully updated contribution on the "Fossil Record of Miocene Hominoids" directly connects with Godinot's and discusses the adaptive radiations of hominoids and hominoid-like primates. The author describes this period as the "golden age of the Hominoidea" (re his definition of this taxon, see our comment in the preface of the first edition), when some basic attributes of our forerunners appeared, e.g., the absence of a tail, a somewhat extended life history, a slightly enlarged level of encephalization, and hints of powerful hand and foot grips and a propensity for more vertical climbing. Begun presents the latest data on the split between the hominines in the west and the pongines in the east and describes the evolution of the African apes and humans and the appearance of the *Pongo* clade. Of special paleoanthropological interest is that shortly after their dispersal into Africa, hominines diverged probably relatively quickly into their respective clades. Begun's review of the fossil record of hominoid evolution suggests to him "that humans evolved from a knuckle-walking, forest-dwelling soft fruit frugivore/omnivore. Not a chimpanzee in the modern sense, but more chimp-like than anything else nonetheless." **Jordi Augustí's** slightly updated article on "The Biotic Environments of the Late Miocene Hominids" gives a vivid impression of the Middle Miocene terrestrial ecosystems with their wide mammalian diversity of taxa chronologically followed by drier conditions and increasing seasonality in some parts of the Old World and a worldwide extension of grasses at 7–8 Ma. Augustí concludes that "at this moment an extension to the south of the Greek-Iranian Province can be recognized, which led to the Plio-Pleistocene savanna biome, characterized by a high diversity of hypsodont bovids, large grazers like rhinoceroses and giraffids and, most probably, the hominoids that led to the first hominins in Africa." However, the question remains open whether hominin ancestors were part of the "Greek-Iranian province" at all. **Carol Ward** has added some current literature and new critical commentary to her valuable review on "Postcranial and Locomotor Adaptations of Hominoids." She sees increasing evidence for "…the hypothesis that homoplasy…has possibly occurred multiple times within the Hominoidea." In contrast to David Begun, she is unconvinced that *Australopithecus* evolved from a highly derived African apelike ancestor adapted to knuckle-walking. Rather, "mounting evidence from the Miocene suggests that the australopith ancestor was orthograde, not a terrestrial quadruped." If this holds true, paleoanthropologists should no longer ask why hominins were selected to stand up on two legs from all fours but change the question to "Why did early hominins remain orthograde when they began exploiting terrestrial niches?"

Ward's discussion provides excellent background to **Alan Bilsborough** and **Todd C. Rae's** extensive contribution on "Hominoid Cranial Diversity and Adaptation," which has been thoroughly updated. Their detailed review of the extraordinary diversity of hominoid craniomorphological structures allows the formulation of hypotheses about the feeding adaptations of earlier hominoids although more detailed analyses fail to show an exact correspondence. In part, this is a consequence of dietary variability and, in part, of cranial variation. Further, just as in Carol Ward's contribution, the homoplasy problem constantly looms because the cranium represents a tightly constrained, functionally and developmentally integrated structure that is subject to multiple selective influences. It is thus not surprising that none of the potential Miocene candidates can be convincingly ascertained as forerunner to any modern ape. This chapter serves as an excellent example of the diverse possibilities as well as the limitations of comparative morphology.

While there are broad associations between African ape diet and cranial form, evidence suggests that cranial features are less closely determined by diet than are characteristics of dentition. **Mark S. Teaford** and **Peter S. Ungar's** dentomorphological approach helps clarify this. Their update of "Dental Adaptations of African Apes" shows how new high-tech methods can help us generate increasing knowledge of the dietary patterns of fossil apes. However, the authors are careful not to overestimate the reliability of such findings since our descriptions of primate diets are invariably oversimplified. Teaford and Ungar emphasize that the key to valid and reliable findings "…lies in the collaborative use of as many lines of evidence as possible, on samples that are as large as possible." They plead for combining dental microwear analyses and other paleobiological indicators to gain new perspectives on the dietary capabilities of the earliest hominins. Future research in this field is very promising as “… the bottom line is that researchers have only begun to tap into a wealth of data from innumerable sources, ranging from laser scanning and dental microtextures to finite element modeling and nanoindentation.”

Dean Falk’s review of “Evolution of the Primate Brain” has been slightly revised and remains a highly informative introduction to this field. She presents general methods for the macromorphological study of primate brain evolution, describes the evolution of the brain size and the cranial capacities of various adult hominins, and discusses the evolution of general neurological reorganization as well as reorganization related to language, handedness, and music. She also reports exciting new results from a comparative analysis of the spacing of neurons in the frontopolar region of apes and hominins. The horizontal spacing distance (HSD) between neurons increased in hominins after they split from chimpanzees, and this is “…interpreted as facilitating complex interconnectivity, which contributes to information processing related to anticipating future events, multitasking, and integrating limbic input to arousal, motivation and intentions, among other functions.” **Elke Zimmermann** and **Ute Radespiel** integrated numerous new findings, data, and literature into their updated contribution on “Primate Life Histories.” Their article is a very useful treatise on our current knowledge on the diversity of primate life histories and current hypotheses on the evolutionary forces that underlie them. **Angela Meder** has integrated the results of several dozen new studies into her discussion of “Great Ape Social Systems.” These deal with such issues as fission-fusion social systems as a strategy for coping with ecological constraints; foraging and ranging behavior during fallback episodes; cooperative breeding and the evolution of our unique features; maternal support, dominance status, and mating success in male bonobos; and lethal intergroup aggression and its impact on territorial expansion in chimpanzees. In spite of the fact that great ape populations have been studied for decades, ape social systems are not yet completely understood and have not so far contributed much to the issue of what the “natural” human mating system is. In pursuit of the central, stable component of human social systems, Meder absorbingly discusses “How Our Ancestors Broke through the Gray Ceiling” (*sensu* Isler & van Schaik).

Joanna E. Lambert surveys the extraordinary diversity of feeding- and foraging-related adaptations among primates. Her expanded title, “Evolutionary Biology of Ape and Monkey Feeding and Nutrition,” reflects the broadening of her focus to include the results of numerous nutritional studies. Indeed, the chapter was partly rewritten to suggest the evolutionary underpinnings and ecological implications of feeding adaptations and to thoroughly demonstrate evolutionary correlations of large brains, trichromatic color vision, and tool use. Furthermore, Lambert stresses the problems involved in fermenting fibers and detoxifying plant chemicals and discusses their implications for primate adaptation since the Miocene. Finally, focusing on hominoid feeding biology, she evaluates our own lineage and critically reviews relevant energetic trade-off hypotheses such as the “social brain hypothesis" and the "expensive-tissue hypothesis" as well as the recently proposed broader "energy-based hypothesis." The similarly enlarged title of **Nicholas E. Newton-Fisher's** contribution on "The Hunting Behavior and Carnivory of Wild Chimpanzees" points to equally extensive revision. It has been known for a long time that chimpanzees are not the only primates that hunt vertebrate prey, but interestingly enough, except for the bonobos, *Pan troglodytes* is the only hunting great ape; vertebrate predation appears to be rare or absent among both gorillas and orangutans. Until now, hunting has seemed to be a ubiquitous aspect of male chimpanzee behavior though there is obvious diversity, i.e., the intensity and frequency of hunting varies between populations as well as chronically and regionally. The value of meat is obvious, providing a compact nutritional package; however, the adaptive question of *why* chimpanzees hunt is still controversial. Current studies increasingly shed doubt on the "meat-for-sex" hypothesis, while the "show-off" and the "hunting-as-a-risk-assessment" hypotheses are gaining increasing support. Newton-Fisher convincingly refutes the notion that chimpanzees switch to hunting to compensate for energy shortfalls and provides arguments in support of the "meat-scrap" hypothesis, which assumes that chimpanzees gain essential micronutrients from small amounts of meat ("scraps") without having to consume vast quantities of plant material. Newton-Fisher empathically stresses the significance of this kind of field research for clarifying "both why chimpanzees hunt and the importance of this behavior for the study of human evolution."

Charlotte K. Hemelrijk, **Ivan Puga-Gonzalez**, and **Jutta Steinhauser's** updated contribution deals with "Cooperation, Coalition, and Alliances" and continues to express severe doubts about the evidence for cooperative altruism and kin selection. These authors continue to believe that a great deal more detailed observation of primates will be needed to evaluate the cognitive complexity inherent in apparent coalition-building behaviors and go a step further with the statement that "behavioral acts, such as grooming, coalition formation, and tolerance during feeding, have originally been considered as 'altruistic' but are presently often considered advantageous for both parties, the actor and receiver." They propose to regard reciprocity as "emotional bookkeeping," which "suggests that the frequency and quality of previous and present social interactions with a particular partner elicits a specific emotional state. This emotional state may lead to reciprocation and interchange of beneficial acts without relying on high cognitive mechanisms." Further, they reassess patterns of reconciliation and consolation that have hitherto been considered to reflect sophisticated cognition. The authors are increasingly convinced "that these patterns may also arise from simple behavioral rules." In 2007, we endorsed **Richard W. Byrne's** prognosis that we would soon approach a possible paradigm change in the study of primate intelligence and cognition, and this seems to be coming about. Byrne's significant contribution on "Primate Intelligence" continues to insist that "…intelligence is not a single 'thing' but rather a mixed bag of devices and processes, endowments, and aptitudes." This conglomerate of separate facets of intelligence makes it extremely difficult to answer key questions like: What triggered the brain size in primate evolution? What pushed the hominins and especially our species into another league? The author sees two separate changes in intellectual potential with concomitant brain changes. Coping with and succeeding within larger groups induced the enhancement of social perception and memory, but "impressive-seeming tactics of behavior such as deception and cooperation," did not allow a "deep understanding of the mechanism of these social tactics" or "show insight into causal relationships in the physical sphere." In Byrne's view, there was a second evolutionary event by which ancestral great apes acquired extra skills "based on their ability to learn novel routines of skilled, bimanually coordinated manual action, sometimes involving tool use, sometimes involving locomotion, and reliant on imitation by behavior parsing as well as exploration." This may have been the basis for understanding the intentions of other individuals and of a rudimentary grasp of the causal logic of physical events. Since there is much debate whether comparative psychology can decipher the evolutionary roots of the "mind-reading" capabilities traditionally regarded as uniquely human, we asked **Juliane Kaminski** to write a contribution on this specific issue. "Theory of Mind: A Primatological Perspective" poses the question of whether nonhuman primates have the ability to attribute mental states to others. Kaminski explains that "members of different primate species seem to follow other individuals' gazes and are sensitive to others' attentional states; there is as yet evidence in only a few species for an understanding of others' visual perspectives, knowledge states, or intentions." The current consensus is that nonhuman primate species don't have the capacity to truly attribute mental states to others. Will further research validate or close the gap?

We are aware that the selected chapters in this volume give only a restricted view on the wide field of primatology, a dynamically expanding evolutionary discipline that is indispensable for an evolutionary understanding of human origins. But we nonetheless hope that the combination presented here of updated, replacement, and new chapters will provide readers with a reasonably comprehensive introduction to the underpinnings of this fascinating subject area. If we have succeeded in doing this, the credit goes entirely to our authors.

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Winfried Henke
Mainz, Germany

Ian Tattersall
New York City, USA

Preface to Volume 3, Second Edition

Phylogeny of Hominins

In this third volume of the *Handbook of Paleoanthropology,* our contributors cover the evolutionary record of Homininae in a roughly chronological sequence, with chapters on various methodological approaches interpolated. As always, we have encouraged authors to emphasize their own points of view while paying due notice to competing ones; and in cases where the field is polarized or highly divided, some chapters deliberately overlap in their coverage. In this second edition, almost all chapters have been replaced or extensively updated, and some additions have been made, as with the chapters on the odd hominid from Flores and on human brain evolution.

George Koufos, in "Potential Hominoid Ancestors for Hominidae," opens the volume with a review of Miocene hominoid taxa that are putatively close to the hominin stem and finds the European record particularly instructive in this regard. Asian Miocene hominoids, on the other hand, group into a pongine clade. **Jeffrey Schwartz** ("Defining Hominidae") follows with a bracing and wide-ranging review of the concept of Homininae (for which he prefers the family rank Hominidae, giving flexibility in the recognition of subclades). He notes a variety of current deficiencies in both the definition and the recognition of the group and suggests a variety of potential postcranial synapomorphies. In contrast, he finds that derived dental features also unite the clade with pongines. In "Role of Environmental Stimuli in Hominid Origins," **Elisabeth Vrba** reviews how external environmental stimuli appear to have influenced hominin evolutionary history and provisionally identifies successive cooling trends over the Plio-Pleistocene as initiators of the *Paranthropus* "hypermasticatory" tendency and the tradition of stone–tool-making at around 2.5 Ma, the adoption of obligate bipedality at around 1.6 Ma, and significant expansions of the brain at around both 2 Ma and 600 Ka. She also emphasizes the implications of climatic oscillation for speciation in the hominin clade. From a more internal viewpoint, **Bogusław Pawłowski** and **Wioletta Nowaczewska** ("Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins") then look more generally at the putative selective pressures that might have shaped the divergence of the hominin lineage from more generalized hominoid trends both in the locomotory and masticatory systems.

The next few chapters are similarly thematic. In a stimulating overview, **Will Harcourt-Smith** ("Origin of Bipedal Locomotion") looks at bipedal locomotion and its anatomical correlates and traces the successive appearances in the hominoid/hominin clades of facultative, habitual, and finally obligate bipedality. He concludes that the most robust explanations for hominin adoption of this unusual locomotor mode lie in external environmental shifts. **Ralph Holloway's** "The Evolution of the Hominid Brain" addresses the evolution of hominin brains and introduces the underlying neurogenomics. Holloway charts the unique hominin history of brain size increase, and in terms of gross morphology takes particular note of the primary visual cortex, the posterior association cortex, cerebral asymmetries, and Broca's area. **David Strait**, **Fred Grine,** and **John Fleagle** ("Analyzing Hominin Phylogeny: Cladistic Approach") next usefully review concepts of phylogeny reconstruction and the various numerical approaches currently employed in this area. They point to an emerging consensus in at least the broader outlines of hominin phylogeny. **Todd Disotell's** "Phylogenetic Relationships of Hominids: Biomolecular Approach" addresses hominin phylogeny in molecular perspective with a wide-ranging review of methods and results that also emphasizes a developing consensus.

With **Brigitte Senut's** "The Miocene Hominoids and the Earliest Putative Hominids," we return to the fossil record. Senut reviews the African Upper Miocene record, concluding that chimpanzees are a poor model for early hominins and that among all putative "earliest hominin" candidates, only *Orrorin tugenensis* shows unequivocal evidence of bipedality. She emphasizes that this form of locomotion arose in mixed rather than open habitats, and suggests based on new fossil finds that the split between African apes and hominins could have occurred much earlier than usually thought. **Bill Kimbel** ("The Species and Diversity of Australopiths") follows with an overview of the australopiths, providing individual portraits of each of the species currently recognized. He warns that the australopith fossil record is as yet too spotty to allow a clear view of evolutionary pattern in this group of early hominins, but nonetheless emphasizes its diversity. **Mark Collard** and **Bernard Wood** ("Defining the Genus *Homo*") then turn our attention to the genus *Homo*, and how it should be defined and recognized. They point out the *ad hoc* way in which this genus has been accreted, and suggest that its growth has got out of hand. They advocate a more compact concept of *Homo* that excludes the species *habilis*, *rudolfensis*, and *floresiensis*. **Friedemann Schrenk**, **Ottmar Kullmer**, and **Tim Bromage** follow up on this in "The Earliest Putative *Homo* Fossils," overviewing the various fossils that have been attributed to "early *Homo*." They are prepared to accept a more comprehensive concept of the genus than Collard and Wood's, and correlate the appearance of this implicitly paraphyletic taxon with that of material culture, at about 2.5 Ma. They believe that the megadont early *Homo* species were adapted to the more arid conditions that began to prevail at this inflexion point of the paleoclimatic curve.

Ian Tattersall ("*Homo ergaster* and Its Contemporaries") points out that the fossils often attributed to "early African *Homo erectus*" exhibit no convincing synapomorphies with the eastern Asian materials that define this species. He further points to a morphological variety in the African record that will have to be addressed systematically at some point. Provisionally, he accepts the name *Homo ergaster* for the African fossils but finds that this species cannot reasonably accommodate the hominin fossils from Dmanisi in the Caucasus, which may themselves not be homogeneous. A completely different interpretation in respect to the systematics and classification of *H. erectus* is presented by **Karen Baab** in her replacement chapter on "Defining *Homo erectus*." She belongs to the group of paleoanthropologists who advocate a *sensu lato* definition for *Homo erectus*, interpreting the considerable morphological and geographic variation within Early and Middle Pleistocene *Homo* fossils as indicating an Old World-wide polytypic species. Her interpretation of the morphological features of the skull leads her to believe that the fossils assigned to *Homo erectus s.l.* maintain "a broadly homogenous cranial and postcranial *Bauplan* across an impressive geographic and temporal range," and she is convinced that the "single species model for *H. erectus* cannot be rejected on the basis of cranial morphology." Readers are encouraged to draw their own conclusions about the "Muddle in the Middle." Not too long ago, many paleoanthropologists still regarded *Homo erectus* as a valid European taxon as well, but **Philip Rightmire** updates this view of "Later Middle Pleistocene *Homo*." He compares and interprets the hominin fossil specimens known from Middle Pleistocene localities in Africa, Europe, South Asia and the Far East, and argues that fossils such as those from Bodo, Kabwe, Arago, Petralona, and Dali retain many plesiomorphic *erectus*-like characters but had undergone a speciation event in which *H. erectus* gave rise to a daughter lineage. Rightmire favors anagenetic change here, asserting that "differences between the Middle Pleistocene hominins can be attributed to geography, time, or intragroup variation. Many, if not all, of the European and African specimens can be accommodated in one species distinct from Neanderthals and modern humans." While he advocates for *Homo heidelbergensis* as the appropriate name of the taxon, which is "probably ancestral to both the Neanderthals in Europe and the earliest representatives of *H. sapiens* in Africa," he cites new craniodental research on the Sima de los Huesos sample suggesting that this population "…may constitute a source population for Neanderthals, while Mauer and Arago document the presence of a morphologically distinct lineage."

Katarina Harvati's extensively updated review of "Neanderthals and Their Contemporaries" forcefully shows that even the longest-running debate in paleoanthropology, namely, the status of the Neanderthals, can still trigger vivid controversies. The current debate partly concerns whether the Sima de los Huesos hominins should be considered early (Pre-)Neanderthals, instead of *H. heidelbergensis* as the discoverers have inexplicably proposed. Her conclusion is that if "the European *H. heidelbergensis* was exclusively ancestral to Neanderthals, this sample could be placed within the Neanderthal lineage and within the taxon *H. neanderthalensis*.... Alternatively, the European lineage could be arbitrarily split into two paleospecies, the earlier segment retaining the nomen *H. heidelbergensis* and the later *H. neanderthalensis*." Harvati also reports and discusses the newest results on Neanderthal genomics, and considers the unprecedented case of the Siberian Denisovans, in which a distinct hominin lineage has been recognized on genomic criteria alone. Just as unusual as the Denisovans was the discovery of a late surviving hominin population in the Liang Bua cave on Flores (Indonesia). **Leslie Aiello** has kindly contributed a chapter on "*Homo floresiensis*" as this population was called by its discoverers. Extremely small-bodied and small-brained, the Flores hominids, dated between 74 Ka and 17 Ka, have been energetically debated. Many are convinced that these fossils are pathological versions of *Homo erectus* or *Homo sapiens*, while others conclude that they represent a distinctive hominid lineage. Aiello thoroughly reviews the various hypotheses about the unique morphology and the relationships of *H. floresiensis* and concludes that the "new species" hypothesis is much more convincing. As to its relationships, she judiciously concludes that "until conclusive evidence appears in the form of additional fossil material, analytical advances, and ideally ancient DNA evidence, [w]e have not heard the end of the *H. floresiensis* story."

Günter Bräuer's updated contribution on "Origin of Modern Humans" overlaps in many respects with issues raised in the preceding chapters as his "Out-of-Africa and Hybridization" model is deeply rooted in Africa. He meticulously analyzes the fossil record and concludes that there was a long-lasting, mosaic-like transition or modernization process in Africa. Participants ranged from 600 Ka-year old fossils like Bodo, classified as "archaic *Homo sapiens*" (grade 1), through an intermediate "late Archaic *Homo sapiens*" (grade 2), to "anatomically modern *Homo sapiens*" (grade 3). This last species replaced archaic populations in other places of the Old World with only slight admixture. Bräuer sees support for his view in recent comparative morphological research and new absolute dates for several hominin specimens, and welcomes current paleogenomic findings such as those from nuclear DNA analyses suggesting widespread if minor archaic-modern hybridization. Bräuer finds these largely in accordance with a lengthy process of modern human origins, without any speciation events. This specifically means we should "regard the European Preneanderthals/Neanderthals and the African Middle Pleistocene lineage to modern humans and the late archaic group in China as belonging to one polytypic species *H. sapiens*." In "Population Biology and Population Genetics of Pleistocene Hominins," **Alan R. Templeton** discusses three types of molecular data analysis: "coalescent processes and haplotype trees estimated from surveys of genetic variation in present-day human populations, haplotypes inferred from ancient DNA extracted from fossils, and overlays of current quantitative genetic variance/covariance matrices upon hominin fossils." He discusses with admirable clarity the complex issues involved, such as nested clade phylogeographic analyses, demographic inferences from coalescent analyses; demic diffusion; admixture; isolation by distance; positive selection. In spite of much progress in paleogenomics, Templeton finds himself able to maintain the basic conclusions presented in the earlier edition.

Michael Bolus asks: What does the archaeological record contribute to our knowledge of dispersal patterns? Reviewing "Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Bolus traces assumed dispersal routes by analyzing the diverse artifact assemblages and reconstructs the different waves "out of Africa" to Eurasia, Eastern and Southeastern Asia, and finally to Sahul and Europe. Up to now, the 1.8 Ma Dmanisi hominids are the earliest outside Africa, and Bolus suggests that slightly younger evidence from Southeastern and eastern Asia also traces to the same first wave of expansion. He sees the Levantine Corridor is regarded as one of the major dispersal routes for early humans, although a southern route through the Arabian Peninsula seems possible. Bolus describes the dispersal of the Oldowan and reports that the late occurrence of this techno-complex at Atapuerca (Spain) is probably due to a later expansion wave. The Acheulean started in Africa some 1.8 myr ago, and reached southern Asia much earlier than Europe, where the earliest secure appearances are not older than 700–600 Ka. Bolus also looks at the techno-complexes of the Neanderthals and their apparent overlaps in the Near East with those of anatomically-modern *Homo*.

In July of last year, we received the sad news of the passing of our friend **Christy G. Turner II**, "father of dental anthropology" and a prolific and influential anthropological researcher. We are happy that Christy's coauthor, **G. Richard Scott**, agreed to update their joint contribution on "Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia." The earliest colonization of the Americas is still intensively debated, and, despite its title, this updated review also integrates biological data including nuclear markers, mtDNA, Y-chromosome, and craniometrical sources, that bear on the peopling of the Americas. Significantly, "the homogeneity among American Indians indicated by dental morphology is paralleled by mtDNA and Y chromosome haplogroup data and single-nucleotide polymorphism (SNP) arrays."

Nick Toth and **Kathy Schick's** valuable and compact "Overview of Paleolithic Archaeology" has been updated by integrating much new evidence on technological change and cognitive complexity from paleoanthropology and primatology into their archaeological perspective. They summarize archaeological advances from the earliest, ca. 2.6 Ma evidence of hominin technology in the Ethiopian Rift Valley, to early occupation of the Americas by at least 15 Ka. They conclude that "the human lineage is a product of its Paleolithic past, and that the modern human condition, characterized by industrialization, farming, urban life, and ever-increasing networks of communication and globalization, is firmly rooted in its Stone Age past." **Nicholas Conard's** chapter on "Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia" connects to this same issue, especially in focusing on the "large-scale patterns of behavioral change that are often viewed as indicators for the advent of cultural modernity and developed symbolic communication." His update, including several amazing new figures, uses examples from Africa and Eurasia to review patterns of lithic and organic technology, subsistence, and settlement as potential indicators of modern behavior. In discussing hypotheses for the development and spread of cultural modernity, he rejects a strict monogenetic model in favor of a pattern of mosaic polycentric development. This chapter highlights the need for new refutable, regional and superregional hypotheses for the advent and spread of behavioral modernity.

The final two chapters deal with entirely different aspects of the unique modern human behavioral pattern. Every human society practices religion, and there is consensus that religiousness is part of the canon of transcultural human universals (which, though descriptive, are not definitional). This is reason enough to inquire into whether religiosity might have any evolutionary implications and/or adaptive value. **Matthias Herrgen**, philosopher and anthropologist, contributes reviews of "Evolution of Religion" that aims to provide a naturalistic foundation for religious behavior. Herrgen's focus is on emergent features of cultural evolution, e.g., on mysticism, ethics, myth, and ritual as domains of religion. He assumes that these domains describe a modular structure of cognitive skills in a network of brain, body, language, and culture that provides an architecture underlying the human capacity for religion. He concludes that "the vast bio-cultural complexity must be the key aspect in any theory of the evolution of religion. Concepts like the (cognitive) niche construction offer new perspectives in the gene-culture-coevolution for further approaches to the study of religion." The final contribution to this new edition of the *Handbook of Paleoanthropology* is an extended update of **Mathias Gutmann** and **Michael Weingarten**'s contribution on "Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology." Inspired by the vivid interdisciplinary discussion stimulated by the 200th anniversary of Charles Darwin's birth, Gutmann and Weingarten have framed their essay to explain, within a criteriological framework, which traits should be considered "typically human." With this approach, "the difference between human and nonhuman beings is expressed in terms of an animal-human comparison." The authors' mediation-oriented perspective assumes "that the nonhuman-human transformation takes place not within (first) nature but within culture," which has "consequences for empirical research as well as for ethical judgment." Their considerations confront us with the dilemma that paleoanthropology as a biological discipline cannot provide us with an adequate basis for ethical reasoning, while "on the other hand those ethical approaches, which depend immanently on criteriological descriptions of humanity, show serious methodological deficiencies."

As with the other volumes of the *Handbook*, we hope that the reader will find in these pages a useful and reasonably comprehensive resource for understanding the current state of knowledge and debate in the area it covers of the multifaceted study of paleoanthropology. Once again, we thank our contributors and emphasize that any deficiencies the reader may find are ours.

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Winfried Henke
Mainz, Germany

Ian Tattersall
New York City, USA

Editors

Winfried Henke
Institut für Anthropologie (1050)
Fachbereich 10 – Biologie
Johannes Gutenberg-Universität Mainz
D-55099 Mainz
Germany
and
Lion-Feuchtwanger-Str. 57
D-55129 Mainz
Germany
henkew@uni-mainz.de

Winfried Henke is retired Academic Director and apl. Professor of Anthropology at the Johannes Gutenberg University of Mainz. He was born in 1944 in Pomerania, Germany, and studied biology, anthropology, geosciences, as well as philosophy and pedagogy in Kiel and Braunschweig. In 1971, he received his Ph.D. (Dr. rer. nat.) from the University of Kiel, his thesis focusing on a prehistoric anthropological topic and multivariate statistical analysis in skeletal biology. Since 1971, Henke conducted research and taught at the Faculty of Biology of the Johannes Gutenberg University of Mainz in paleoanthropology, primatology, prehistoric anthropology, comparative morphology, systematics, demography, sociobiology, and scientific history. He had research activities in various countries (Iceland, Israel, Jordan, US, Greece), and in 1990, he habilitated with a monograph on the "Anthropology of Upper Paleolithics and Mesolithics of Europe and the Mediterranean Basin." In the scope of the ERASMUS docent exchange program, intensive lecturing at numerous European Universities followed. Henke acted as elected anthropology referee for the German Research Foundation (DFG) and still serves at the advisory boards of scientific journals (e.g., *Interdisziplinäre Anthropologie*, published at Springer-Verlag); further, he was book review editor and advisory consultant to museums, e.g., the Neanderthal Museum (Germany). He published approximately 200 original papers in scientific journals and anthologies and several hundreds of book reviews and supervised more than 100 diplomas and Ph.D. theses in biological anthropology. He is author, coauthor (together with H. Rothe), and editor of several books including such standard works as *Paläoanthropologie*, *Stammesgeschichte des Menschen*, and *Phylogenetische Systematik* (published at Springer-Verlag). In 2006, he was awarded the honorary doctorate of the National and Kapodistrian University of Athens; he is an elected member of the German National Academy of Sciences *Leopoldina* and Academician of the *Leibniz-Sozietaet of Sciences.*

Ian Tattersall
Division of Anthropology
American Museum of Natural History
New York, NY 10024
USA
iant@amnh.org

Ian Tattersall is Curator Emeritus in the Division of Anthropology of the American Museum of Natural History in New York City. Trained in archaeology and anthropology at Cambridge and in geology and vertebrate paleontology at Yale, he has worked on lemur systematics and ecology as well as in paleoanthropology, where his special interest has been in hominid diversity and cognitive evolution. Most recently, he has been concerned with trying to understand how a nonlinguistic and nonsymbolic ancestor gave rise to the cognitively unprecedented *Homo sapiens* and what drove the exceptionally fast evolution of the human lineage over the course of the Pleistocene. He has done both primatological and paleontological fieldwork in countries as diverse as Madagascar, Vietnam, Surinam, Yemen, and Mauritius. In collaboration with Jeffrey Schwartz, he wrote three volumes of *The Hominid Fossil Record* (2002–2005), a documentation in standardized descriptive and illustrative format of a large proportion of the most significant fossils that tell the human evolutionary story. Ian is also a prominent interpreter of human paleontology to the public with several trade books to his credit, among them *The Brain: Big Bangs, Behaviors, and Beliefs* (2012, with Rob DeSalle), *Masters of the Planet* (2012), *Race? Debunking a Scientific Myth* (2011, with Rob DeSalle), *The World from Beginnings to 4000 BCE* (2008), *Becoming Human: Evolution and Human Uniqueness* (1998), and *The Fossil Trail: How We Know What We Think We Know About Human Evolution* (1995, 2nd ed. 2009), as well as many articles in *Scientific American* and *Natural History* and the coeditorship of the definitive *Encyclopedia of Human Evolution and Prehistory*. He lectures widely and, as curator, has also been responsible for several major exhibits at the American Museum of Natural History including *Ancestors: Four Million Years of Humanity* (1984); *Dark Caves, Bright Visions: Life In Ice Age Europe* (1986); *Madagascar: Island of the Ancestors* (1989); *The First Europeans: Treasures from the Hills of Atapuerca* (2003); and the highly acclaimed *Hall of Human Biology and Evolution* (1993) and its successor, *Hall of Human Origins* (2007).

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Contributors

Jordi Agustí ICREA-Institute of Human Paleoecology, Universitat Rovira i Virgili, Tarragona, Spain

Leslie C. Aiello Wenner-Gren Foundation, New York, NY, USA

Karen L. Baab Department of Anatomy, Midwestern University, Glendale, AZ, USA

David R. Begun Department of Anthropology, University of Toronto, Toronto, ON, Canada

Paolo Biagi Department of Asian and North African Studies, Ca' Foscari University – Venice, Venezia, Italy

Alan Bilsborough Department of Anthropology, University of Durham, Durham, UK

Jonathan I. Bloch Florida Museum of Natural History, University of Florida, Gainesville, FL, USA

Michael Bolus Heidelberg Academy of Sciences and Humanities, Research Project ROCEEH at the University of Tübingen, Tübingen, Germany

Doug M. Boyer Biological Sciences Building, Duke University, Department of Evolutionary Anthropology, Durham, NC, USA

Günter Bräuer Abteilung für Humanbiologie, Universität Hamburg, Hamburg, Germany

Timothy Bromage Department of Biomaterials and Biomimetics, New York University, College of Dentistry, New York, NY, USA

Daniel R. Brooks Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, ON, Canada

Richard W. Byrne Centre for Social Learning & Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, Scotland, UK

Mark Collard Human Evolutionary Studies Program and Department of Archaeology, Simon Fraser University, Burnaby, BC, Canada

Department of Archaeology, University of Aberdeen, Aberdeen, UK

Nicholas J. Conard Eberhard–Karls–Universität Tübingen, Institut für Ur– und Frühgeschichte, Abteilung Ältere Urgeschichte und Quartärökologie, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Tübingen, Germany

John A. Van Couvering Micropaleontology Press, Queens, NY, USA

Todd R. Disotell Department of Anthropology, Center for the Study of Human Origins, New York University, New York, NY, USA

Walter Etter Abteilung Geowissenschaften, Naturhistorisches Museum Basel, Basel, Switzerland

David C. Evans Department of Biology, University of Toronto at Mississauga, Mississauga, ON, Canada

Dean Falk Department of Anthropology, Florida State University, Tallahassee, FL, USA

School for Advanced Research, Santa Fe, NM, USA

John G. Fleagle Department of Anatomical Sciences, Stony Brook University, School of Medicine, Stony Brook, NY, USA

Kaila E. Folinsbee Department of Anthropology, Iowa State University, Ames, IA, USA

Jörg Fröbisch Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany

Marc Godinot Ecole Pratique des Hautes Etudes and Muséum National d'Histoire Naturelle, Paris, France

Frederick E. Grine Department of Anthropology, State University of New York, Stony Brook, NY, USA

Department of Anatomical Sciences, Stony Brook University, School of Medicine, Stony Brook, NY, USA

Colin Groves School of Archaeology & Anthropology, Australian National University, Canberra, ACT, Australia

Gisela Grupe Department of Biology I, Anthropology, Ludwig-Maximilian-University München, Planegg-Martinsried, Germany

Mathias Gutmann Institut für Philosophie, KIT – Karlsruhe Institute of Technology (Universität Karlsruhe TH), Karlsruhe, Germany

Miriam N. Haidle Research Center "The Role of Culture in Early Expansions of Humans", of the Heidelberg Academy of Sciences and Humanities, Senckenberg Research Institute, Frankfurt/Main, Germany

Michaela Harbeck Bavarian State Collection of Anthropology and Palaeoanatomy, Munich, Germany

William E. H. Harcourt-Smith Department of Anthropology, Lehman College CUNY, Bronx, NY, USA

Department of Anthropology, The Graduate Center CUNY, New York, NY, USA

Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY, USA

Britta Hardt Institut für Anthropologie (1050), Johannes Gutenberg-Universität Mainz, Mainz, Germany

Thorolf Hardt Museum, Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany

Donna Hart Department of Anthropology, University of Missouri, St. Louis, MO, USA

Katerina Harvati Paleoanthropology, Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

Charlotte K. Hemelrijk Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, CC, The Netherlands

Helmut Hemmer Institut für Zoologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany

Winfried Henke Institut für Anthropologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany

Matthias Herrgen Philosophisches Seminar, Westfälische Wilhelms–Universität Münster, Münster, Germany

Philosophisches Seminar, Bergische Universität Wuppertal, Wuppertal, Germany

Ralph L. Holloway Department of Anthropology, Columbia University, New York, NY, USA

Jean-Jacques Hublin Department of Human Evolution, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany

Susanne Hummel Institut für Zoologie und Anthropologie, Historische Anthropologie und Humanökologie, Georg-August-Universität Göttingen, Göttingen, Germany

Philippe Huneman Institut d'Histoire et de Philosophie des Sciences et des Techniques, CNRS/Université Paris I Sorbonne, Paris, France

Klaus-Dieter Jäger Institut für Prähistorische Archäologie, Martin Luther-Universität Halle, Halle, Germany

Juliane Kaminski Department of Psychology, University of Portsmouth, Portsmouth, UK

William H. Kimbel Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

George D. Koufos Laboratory of Geology and Palaeontology, Department of Geology, Aristotle University of Thessaloniki, Thessaloniki, Greece

Ottmar Kullmer Department of Paleoanthropology and Messel Research, Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany

Joanna E. Lambert The University of Texas, San Antonio, TX, USA

Julia Lee-Thorp Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, UK

Philip Lieberman Brown University, Providence, RI, USA

Gabriele A. Macho Research Laboratory for Archaeology (RLAHA), University of Oxford, Oxford, England

Alan Mann Department of Anthropology, Princeton University, Princeton, NJ, USA

Jonathan Marks Department of Anthropology, University of North Carolina, Charlotte, NC, USA

Robert C. McCarthy Department of Biological Sciences, Benedictine University, Lisle, IL, USA

Angela Meder Berggorilla und Regenwald Direkthilfe, Stuttgart, Germany

Peter R. Menke Institut für Anthropologie (1050), Johannes Gutenberg-Universität Mainz, Mainz, Germany

Janet Monge Department of Anthropology, University of Pennsylvania, Philadelphia, PA, USA

Nicholas E. Newton-Fisher School of Anthropology and Conservation, University of Kent, Canterbury, Kent, UK

Wioletta Nowaczewska Department of Human Biology, University of Wrocław, Wrocław, Poland

Michael Ohl Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Museum für Naturkunde, Berlin, Germany

Hannah O'Regan Department of Archaeology, University of Nottingham, Nottingham, UK

Bogusław Pawłowski Department of Human Biology, University of Wrocław, Wrocław, Poland

Ivan Puga-Gonzalez Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, CC, The Netherlands

Ryan L. Raaum Department of Anthropology, Lehman College and The Graduate Center, The City University of New York, Bronx, NY, USA

The New York Consortium in Evolutionary Primatology (NYCEP), New York, NY, USA

Ute Radespiel Institut für Zoologie, Tierärztliche Hochschule Hannover, Hannover, Germany

Todd C. Rae Department of Life Sciences, University of Roehampton, London, UK

Kaye E. Reed School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, AZ, USA

Gregory Retallack Department of Geological Sciences, University of Oregon, Eugene, OR, USA

Daniel Richter Department of Human Evolution, MPI Evolutionary Anthropology, Leipzig, Germany

LS Geomorphology, University of Bayreuth, Bayreuth, Germany

Olivier Rieppel Department of Geology, The Field Museum, Chicago, IL, USA

G. Philip Rightmire Department of Human Evolutionary Biology, Harvard University, Peabody Museum, Cambridge, MA, USA

John Rowan School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, AZ, USA

Eric J. Sargis Department of Anthropology, Yale University, New Haven, CT, USA

Kathy Schick Stone Age Institute and Indiana University, Bloomington, IN, USA

Stefan Schlager Department of Anthropology, Faculty of Medicine, Freiburg University Medical Center, Albert-Ludwigs-University Freiburg, Freiburg, Germany

Tyede H. Schmidt-Schultz Department of Biochemistry, University Medical School Göttingen, Göttingen, Germany

Friedemann Schrenk Department of Paleoanthropology and Messel Research, Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany

Michael Schultz Department of Anatomy, University Medical School Göttingen, Göttingen, Germany

Jeffrey H. Schwartz Departments of Anthropology and History and Philosophy of Science, University of Pittsburgh, Pittsburgh, PA, USA

G. Richard Scott Department of Anthropology, University of Nevada, Reno, NV, USA

Brigitte Senut Sorbonne Universités – CR2P – MNHN, CNRS, UPMC-Paris 6, Département Histoire de la Terre, Muséum National d'Histoire Naturelle, Paris, France

Mary T. Silcox Department of Anthropology, University of Toronto Scarborough, Toronto, ON, Canada

Matt Sponheimer Department of Anthropology, University of Colorado at Boulder, Boulder, CO, USA

Jutta Steinhauser Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Groningen, CC, The Netherlands

David Strait Department of Anthropology, University at Albany, Albany, NY, USA

Robert W. Sussman Department of Anthropology, Washington University at St. Louis, St. Louis, MO, USA

Ian Tattersall Division of Anthropology, American Museum of Natural History, New York, NY, USA

Mark F. Teaford Department of Physical Therapy, High Point University, School of Health Sciences, High Point, NC, USA

Alan R. Templeton Department of Biology, Washington University in St. Louis, St. Louis, MO, USA

Department of Evolutionary and Environmental Biology, University of Haifa, Haifa, Israel

Nicholas Toth Stone Age Institute and Indiana University, Bloomington, IN, USA

Linda A. Tsuji Department of Biology, University of Washington, Seattle, WA, USA

Alan Turner Deceased. Formerly at School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK

Christy G. Turner II Deceased. Formerly at School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

Peter S. Ungar Department of Anthropology, University of Arkansas, Fayetteville, AR, USA

Elisabeth S. Vrba Department of Geology and Geophysics, Yale University, New Haven, CT, USA

Guenther A. Wagner Geographisches Institut, Universität Heidelberg, Heidelberg, Germany

Carol V. Ward Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, MO, USA

Gerhard W. Weber Department of Anthropology, University of Vienna, Wien, Austria

Michael Weingarten Institut für Philosophie, Universität Stuttgart, Stuttgart, Germany

Ursula Wittwer-Backofen Department of Anthropology, Faculty of Medicine, Freiburg University Medical Center, Albert-Ludwigs-University Freiburg, Freiburg, Germany

Bernard Wood Center for the Advanced Study of Human Paleobiology, Department of Anthropology, George Washington University, Washington, DC, USA

Human Origins Program, Smithsonian Institution, Washington, DC, USA

Franz M. Wuketits Institut für Philosophie, Universität Wien, Wien, Austria

Elke Zimmermann Institut für Zoologie, Tierärztliche Hochschule Hannover, Hannover, Germany

Part I

Principles, Methods, and Approaches

Historical Overview of Paleoanthropological Research

Winfried Henke

Contents

W. Henke (✉)
Institut für Anthropologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany
e-mail: henkew@uni-mainz.de

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Abstract

This chapter provides a comprehensive scientific historical overview of paleoanthropology as a multifaceted biological discipline. A brief summary of pre-Darwinian theories of evolution is followed by a historical report of the paradigmatic change wrought by Darwin's perspective on life processes, from a teleological to a teleonomic view. Focusing on the fossil discoveries in Europe and later on in Asia and Africa, and on various methodological approaches, it becomes obvious that, as opposed to other biological disciplines, paleoanthropology remained until post-World War II first and foremost a narrative discipline, with widespread contemporary preconceptions (e.g., Eurocentrism, ethnocentrism) as well as erroneous conceptualizations (e.g., typological approach, orthogenism) that set it in many ways apart from the mainstream of biological thinking. Paleoanthropology is widely believed to have maintained this "iridescent image," wrongly, as I will hopefully show. However, there remains skepticism that current theories of human origins are free of narrative components. Since Sherwood L. Washburn provided his innovative conceptual outline for physical anthropology, a theoretical and methodological change has arisen in the understanding of human evolution, focusing on evolutionary adaptations within the order Primates. The anthropological subdiscipline of paleoanthropology profited tremendously from this new approach – albeit with some delay, maybe caused by problems with the "Modern Synthesis" (e.g., the "single species hypothesis"). Intensified exploitation of old and new sites, the improvement of excavation techniques, and complex laboratory research on hominid fossils, on the one hand, and comparative research on living primates (e.g., taxonomy, biomechanics, behavioral psychology, ethology, molecular genetics, and genomics), on the other, constituted paleoanthropology as a highly innovative subdiscipline within the evolutionary sciences seeking to explain the processes of hominization, including our evolution, by concise hypothesis testing. A profound historiographical look back, as we move forward, seems helpful for different reasons: In this way, perhaps we will become more critical about the reliability and validity of our theoretical concepts, methodological approaches, and empirical basis. The history of paleoanthropology could thus help to increase the credibility of ideas about our evolutionary origins.

Introduction

Historical Research: More than Looking into a Mirror!

"Does disciplinary history matter?" This question was asked by Corbey and Roebroeks (2001a, p. 1) at the eponymous congress focusing on the history of paleoanthropology and archaeology. A negative answer assumes that studying the history of these scientific fields is an unsuitable job, at best a nice leisure time activity for retired colleagues. And since Landau (1991) implies in her book on

Narratives of Human Evolution that modern paleoanthropologists are still only "storytellers," a history of paleoanthropology faces a double-sided problem: We have to ask whether there is really any need for a dubious historical approach to a biological discipline that only alleges to be doing science.

The allegation that paleoanthropology is not a serious and respectable field of research is unacceptable, as I hope that the broad spectrum of genuine research presented in the diverse contributions of this handbook of paleoanthropology is proof of this, although this anthropological subdiscipline may have its discreditable aspects (White 2000; Kalb 2001; Stoczkowski 2002; Henke 2010a, b; Reader 2011; more on this later).

In addition, what should one say about the history of science in general? Is disciplinary history no more than a waste of time for practitioners, as well as historians of science? Experience shows that there is no uniform answer to this question. Willoughby (2005) mentions correctly that the historical sciences are different from the so-called hard sciences in which assumptions can be tested experimentally; but even biology is no physics. Popper described evolutionary biology as a "metaphysical research program" and "a possible framework for testable scientific hypotheses" as Tattersall (2002, p. 14) mentions in his sophisticated essay "The Monkey in the Mirror." Though the distinction between the so-called hard and soft sciences has been made for a long time, and anthropology is positioned on the soft side, we have become increasingly aware from recent epigenetic findings (Jobling et al. 2004; Sassone-Corsi and Christen 2012) that the "white coat group" has similar epistemological problems (Oeser 2004). Obviously, scientists need support from philosophers. In his essay *Über die Unvermeidlichkeit der Geisteswissenschaften*, the German philosopher Odo Marquard (1987) emphasized the compensatory function of the cultural sciences and pleaded for the "*Inkompetenzkompensationskompetenz*" [I confess I like this term] of his discipline (Marquard 1974). It think it's a gross error in European curricula of the biological sciences to have marginalized a *propaedeuticum logicum* as merely soft skills.

Let's come back to the historical sciences and their relevance for paleoanthropology. Willoughby (2005, p. 60) summarizes: "Rather than worrying about 'physics envy' (Gould 1981 (sic!), p. 113), some historical sciences are beginning to learn how to live within these restrictions." And this seems to be right for the following reasons: If paleoanthropologists and historians of science can provide good suggestions for the improvement of the discipline, why should one give up studying the history of sciences or look on this discipline as an insignificant one? Goodrum (2009, p. 349) concludes in his valuable contribution to *The History of Human Origins Research*: "Historians, philosophers, and sociologists of science have a great deal to contribute to a better understanding of the development of palaeoanthropology as a science and to the impact it has had on modern culture and society."

Ernst Mayr (1904–2005) – an outstanding modern Darwinist – gave a reasonable, albeit not exhaustive, classification of the various relevant historical approaches: (1) elaborated lexicographic histories, (2) chronological histories,

(3) biographical histories, (4) cultural and sociological histories, and (5) problematic histories (Mayr 1982). The essential point of all these is that the historicist approach may give rise to reflection, as Bowler (1976, 1988, 1996, 1997, 2001), Wolpoff and Caspari (1997), Spencer (1997), Theunissen (2001), Stoczkowski (2002), Delisle (2007), Goodrum (2009, 2013), and Gundling (2005) emphasize.

Although some may doubt whether the various approaches they suggest (heuristics, source criticism, interpretation, hermeneutics, and analytics) will improve paleoanthropology, Corbey and Roebroeks (2001a) emphasize the heuristic value of historical studies. Dennell sees two further lessons from science history: awareness of the dangers of fragmentation and complacency. He considers the lack of dialogue and understanding between the anthropological disciplines as a fatal risk and warns that “There is still excessive specialisation and insufficient dialogue across the disciplines, especially where the terminology and techniques are unfamiliar” (Dennell 2001, p. 66). Concerning the aspect of complacency, he explains that “It is always much easier to see the danger in retrospect, but perhaps one of the main lessons to absorb from the history of science is the danger of too many people becoming too comfortable for too long with an idea, just because so many agree with it, and have agreed with it so often in the past” (Dennell 2001, p. 66). Stoczkowski (2002, p. 197) insists that “we must not forget that the past, remote as it may be, acts on us with a force no less powerful than that of the present. [. . .] Acknowledging that historical processes can be slow and protracted, that timelags due to the force of inertia are omnipresent, that the ideas of yesterday and the day before weigh on those of the present, does in fact offer a few practical consequences, not only on the historian but also to any scientists who seek a better mastery of their conceptual tools.” And Goodrum (2009, p. 338) touches on another relevant aspect when expressing the hope that historiographical studies “can help bridge the gap that sometimes appears to exist between the history of natural sciences and the history of the human sciences.”

I am convinced that a view across the fence between natural and cultural sciences is both necessary and long overdue (see Riedl 1985, 2003; Sarasin and Sommer 2010). The above severe arguments for the improvement of science by disciplinary history are valid for every field of study or “area of intellectual endeavour that holds a common set of concerns, theories, and procedures or techniques that are intended to address a closely connected web of problems” (Shipman and Storm 2002, p. 108). The Darwin anniversary in 2009, with innumerable interdisciplinary colloquia on evolutionary biology and a flood of “Darwinia,” demonstrated that there is an ongoing dialogue which longs for “a cross-fertilization of the various theoretical approaches” as “the crucial step towards a thorough understanding the evolutionary history of our science” (Destro-Bisol and Paine 2011; further Delisle 2007; Henke 2010a, b; Henke and Herrgen 2012; Begun 2013; Goodrum 2013).

A major aspect of biological anthropology is that the present is inevitably rooted in the past. For this reason, Dennell (2001, p. 65) sees the study of human origins as “a search for windows that should give us access to the past through fossil specimens, stratigraphic and climatic changes, inferences from the world

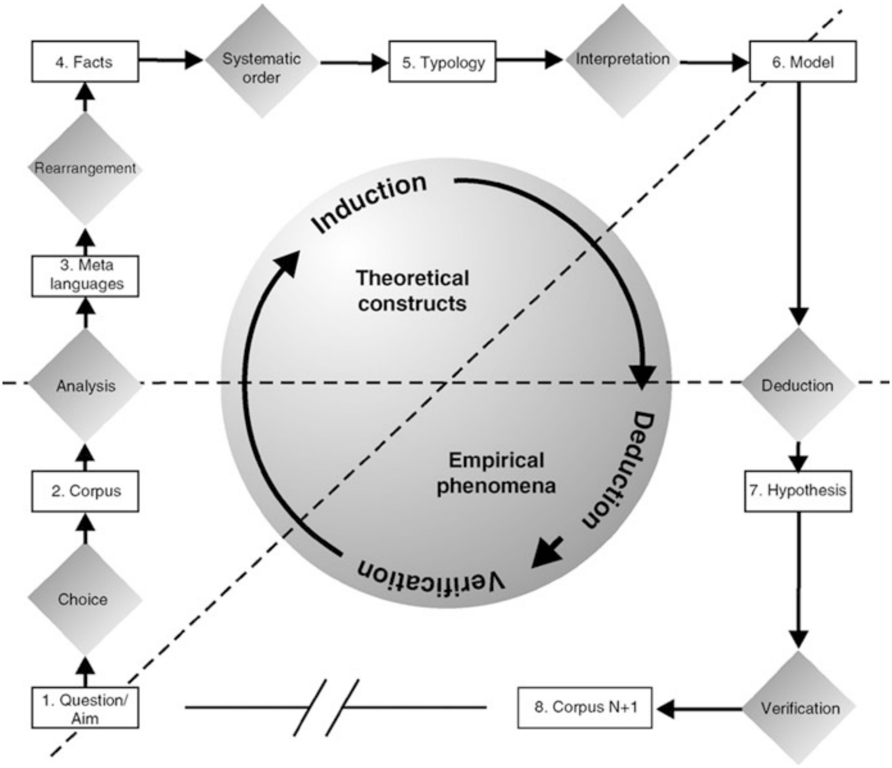
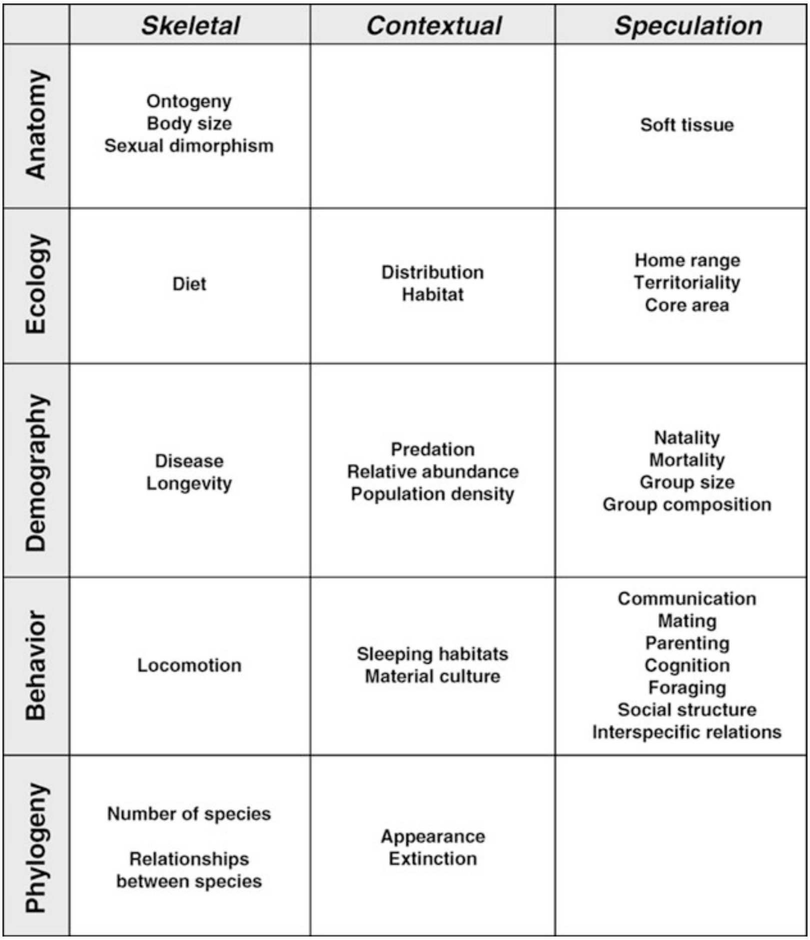


Fig. 1 Diagrammatic relationships between inductive and deductive scientific approaches (After Galley 1978, modified, see Henke and Rothe (1994))

around us, and the like." Paleoanthropologists and prehistorians and archaeologists seek windows to the past but use different sets of keys. A fatal danger is, however, that we may mistake a mirror for a window and simply extrapolate our own views and prejudices about the present onto the past. The important point here is, as L.P. Hartley put it: "the past is a foreign country, they do things differently there" (Foley 1987, p. 78). For this reason, Foley maintains that "The past cannot just be invented or imagined, nor reconstructed solely from observations of the way the world is at the present." This brings both the task and the challenge of paleoanthropological research and other evolutionary sciences to the fore: We are creating essential models (Foley 1987; Henke and Rothe 1994; McHenry 1996; Delson et al. 2000; Stoczkowski 2002; Gutmann et al. 2010; Henke 2003a, b, 2004, 2005, 2007a, b, 2009, 2010a, b, c; Henke and Hardt 2011; Henke and Herrgen 2012). This kind of approach (Figs. 1 and 2) is by no means simply narrative; it is rather contextual hypothesis testing; and even if in some cases it involves scientific speculation, the accent is still on science (White 1988; Henke and Rothe 1994; Henke 2003a). Every scientist needs to arrive at innovative solutions within a channeled imagination. Tattersall (2002, p. 3) stresses in this context: "Indeed,



	Skeletal	*Contextual*	*Speculation*
Anatomy	Ontogeny Body size Sexual dimorphism		Soft tissue
Ecology	Diet	Distribution Habitat	Home range Territoriality Core area
Demography	Disease Longevity	Predation Relative abundance Population density	Natality Mortality Group size Group composition
Behavior	Locomotion	Sleeping habitats Material culture	Communication Mating Parenting Cognition Foraging Social structure Interspecific relations
Phylogeny	Number of species Relationships between species	Appearance Extinction	

Fig. 2 An illustration of how skeletal and contextual data from the fossil records might be used to understand five broad overlapping categories of early hominins (After White 1988, redrawn)

there *is* no single scientific method. Scientific methods of course there are, in abundance; and methodologies lie at the heart of the immense variety of different things that scientists do [but] there is no particular method that will give you the key to all types of scientific inquiry."

The gift of Darwin's theory is "that there was no blueprint to be followed, only unfoldings of opportunity," as Howells (1993, p. 14) put it. If the magnificent panoply of life today is the outcome of a real historical-genetic process without a plan, how do we explain the patterns and processes? Darwin's theory is uncontested as the center of the whole science of biology. In *Darwin's Dangerous Idea*, Dennett (1995, blurb) compares the theory of evolution to a universal acid, an imaginary "liquid that is so corrosive that it will eat through anything!" and asks

"Is nothing sacred?" Every traditional concept that tries to explain our existence has to compete with Darwin's revolutionized worldview. As a consequence of Darwin's theory of life, even human beings can no longer be explained in a teleological way, as expressed by Dobzhansky (1973, p. 125) in his famous dictum: "Nothing in biology makes sense except in the light of evolution".

Common sense mainly considers paleoanthropology as the study of human fossils and a descriptive and broadly narrative discipline that is dominated by poorly researched and media-friendly fossils and findings that cause changing views on the process of human evolution. Particularly, popular science media convey the impression that paleoanthropology is scarcely more than storytelling, labeling every human fossil as spectacular despite the fact that, when viewed soberly, most of the fossils and findings are just as expected. And empirical studies show that the public interest mostly fades very soon or bursts like a soap bubble. But is the history of paleoanthropology in fact something more than the demonstration of "a road full of errors, freak opinions and bizarre concepts finally discarded?" (Corbey and Roebroeks 2001a, p. 1) Or, as Stoczkowski (2002, p. 2) comments: "The problems of origins of humanity and culture, constantly pondered over millennia, provides a convenient opportunity for reconstructing a naive anthropology widely accepted in western culture. This may enable us to retrace the influence exerted by this shadowy knowledge on present day scholarly thought." Given that we are in a dilemma of subject-object identity, we should be conscious of the baggage we carry over from "various 'social' factors, such as fashionable theories, paradigms, ideologies and power relations within the scientific community" (Stroczkowski 2010, p. 1). Are most anthropologists even aware of these obstacles? Apparently not. Most paleoanthropologists are largely concerned with "pure facts." Most anthropologists today agree that paleoanthropology is, like other categories of evolutionary biology, a serious subject involving hypothesis testing and scientific modeling (Wuketits 1978; Foley 1987; White 2000; Wood and Richmond 2000; Wood and Lonergan 2008; Cartmill and Smith 2011; Begun 2013). They are aware that data ascertained from fossils do not speak for themselves and that for this reason the scientific approach involves the creation and testing of hypotheses and theories (Fig. 3). It is by doubting theoretical insights that we come to questioning; and by questioning, we may perceive the truth – or what we think to be the truth (Popper 1959a, b, 1968, 1983; Foley 1987; Mahner and Bunge 2000; Vollmer 2003; Oeser 2004). Stronger theories are those that are optimally corroborated; however, even well-tested general theories may conceivably be refuted (overview in Sarasin and Sommer 2010; Toepfer 2011; Wood 2011). Paleoanthropology is not, like physics, empirical science sensu stricto; but this does not mean at all that it is a narrative subject; storytelling is frowned upon in every science, and I agree with Kroeber (1953, p. 358) who stressed that "there exists basically only one kind of fundamental science. All genuine science aims at the comprehension of reality, and it uses both theory and evidence, in combination, to achieve this comprehension."

In history varying answers have been given to the question "What is the meaning of man?" However, in post-Darwinian times, there is no consensus on how we got

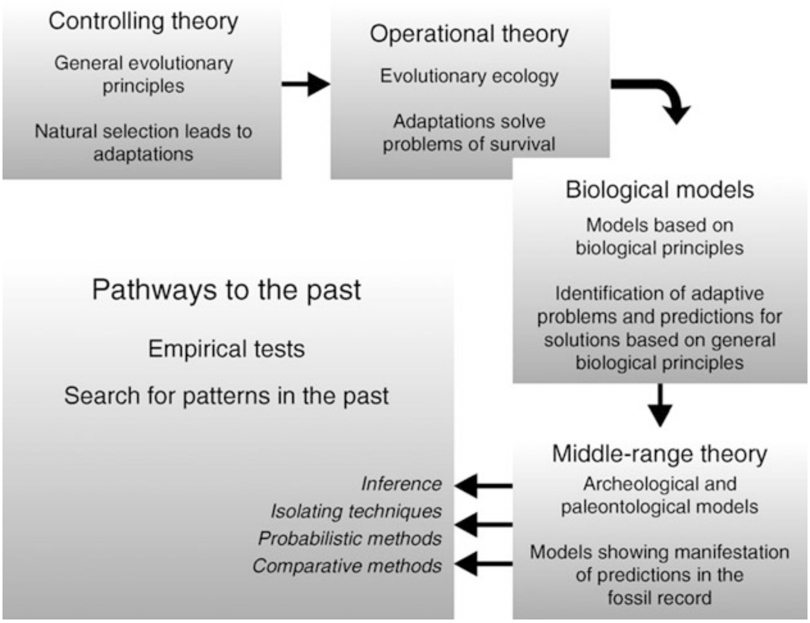


Fig. 3 Pathways to the past; ways of investigating hominid evolution (After Foley 1987, modified)

here (overview in Eldredge and Tattersall 1982; Tattersall 1995, 1998, 2002; Corbey and Theunissen 1995; Antweiler 2009; Bohlken and Thies 2009; Bayertz 2012). Like all other anthropological scientists, paleoanthropologists are only able to establish a reductionistic view of our *conditio humana* (Henke and Herrgen 2012). Heberer (1968a) used the terms "Jetztbild" and "Jeweilsbild" (meaning status quo) to intimate the changeability of our knowledge and the fact that every paleoanthropological report will be out of date very soon after it is published (Hoßfeld 1997, 2005a, b; Schwartz and Tattersall 2002, 2003, 2005). In spite of the multiple schemes in hominin taxonomy and the irritating – not only for laymen and outsiders but for undergraduate students too – various interpretations of the hominid/hominin fossil record (see, e.g., Wood 2000; Wood and Lonergan 2008), there is no doubt that biologists are *in principle* on the right track when evaluating human fossil finds and reconstructing human origin in evolutionary terms (Tattersall 1998, 2002; Delson et al. 2000; Levinton 2001; Grupe and Peters 2003; Cartmill and Smith 2009; Begun 2013).

One word concerning alternative nonbiological explanations of human origin: It is wasting time to discuss pseudoscientific theories of intelligent design proponents at eye level; I am tempted to quote Berthold Brecht: "*Wie kommt die Dummheit in die Intelligenz*?." Biologists have first and foremost to keep their own house clean; however, there is a great interest on the part of historians of science to decipher the reasons and the underlying social and political structures that have recently promoted the renaissance of creationism (Graf 2007, 2010; Graf and Soran 2010; Meyer (2006) for an excellent review and critics, see Neukamm 2009).

Darwin's Perspective on Life Processes

The paradigmatic change from a traditional static view to a dynamic evolutionary concept at the beginning of the second half of the last century resulted in the recognition that humans are an integrated part of a historical process. The so-called Darwinian Revolution, triggered by Darwin's masterpiece from 1859, long remained in a state of confusion. As Bowler (1988) demonstrates in his historiography *The Non-Darwinian Revolution*, Darwin's ideas were fundamentally misunderstood. In his judgment, the impact of evolutionism on late nineteenth-century thought has been greatly overestimated by historiographers (Hull 1973; Moore 1981; Desmond and Moore 1991; Engels 1995; Bowler 1996, 1997, 2001, 2009; Hemleben 1996; Ruse 2005; Goodrum 2004, 2009, 2013; Wuketits and Ayala 2005; Engels and Glick 2008).

Traditionally, it has been assumed that the Darwinian Revolution in biology provided the impetus for a new evaluation of human origins, and Bowler claims that this assumption is valid up to a point. "Because of religious concerns, Darwin and his followers knew that they would have to explain how higher human faculties had emerged in the course of mankind's evolution from the apes" (Bowler 1988, p. 141). The complex scientific answers within the frame of ever-increasing biological facts and the "disciplinary matrix" sensu Kuhn (Chamberlain and Hartwig 1999) essentially reflected our self-image and orientation. An argument often given for the scientific necessity of paleoanthropological research is that humans have to know where they come from to decide where to go; but "How [do] we know what we think we know?" to borrow a phrase from Tattersall's (1995) eponymous book.

Today's paleoanthropology is a subdiscipline of evolutionary biology that aims to describe, analyze, and interpret the process of human evolution, mainly through a vast set of inductive approaches and deductive hypothesis testing (Foley 1987; Henke and Rothe 1994; Wolpoff 1999; Tattersall and Schwartz 2000; Begun 2013). If we want to know more about our origins, there are three basic approaches available to reconstruct our evolutionary history (Washburn 1953; Henke and Rothe 1994, 1999a; Cartmill and Smith 2009):

- First, the primatological approach: One can study the closest living relatives to understand the evolutionary context. Such work includes field and laboratory research on behavior and cognition and comparative morphological, physiological, serological, cytogenetical, molecular biological, and genetic studies (e.g., Goodall 1986; Martin 1990; Jones et al. 1992; Tomasello and Call 1997; Tomasello 1999, 2008; de Waal 2000; Dunbar et al. 2010).
- Second, the paleoanthropological or human paleontological and paleogenetic approach: One can reconstruct our evolutionary history from the recovery and analysis of any relevant fossil evidence, macro- and micromorphological,

histological, and biophysical (e.g., isotopes), and by paleogenetic approaches: ancient mtDNA and genomicDNA (e.g., Aiello and Dean 1990; Herrmann 1986, 1994; Henke and Rothe 1994, 1999a, 2003; Henke 2005; 2010a; Hartwig 2002; Schwartz and Tattersall 2002, 2003, 2005; Hummel 2003; Jobling et al. 2004; Burger 2007; Wagner 2007).

- Third, the population genetic approach: One can study the phenetic and genetic intergroup and intragroup variation of recent human populations to provide clues about geographical samples and their evolutionary histories (e.g., Jones et al. 1992; Freeman and Herron 1998; Jobling et al. 2004; Crawford 2006).
- Finally, there is additional information on prehistoric human activities, mind reading, and symbolism from cultural findings, i.e., the archaeological record, and behavioral fossils (e.g., Haidle 2006; Gamble 1999; Klein 2009; Dunbar et al. 2010; Haidle and Conard 2011; Půtová and Soukup 2015 in press).

Current paleoanthropological research asks not only what our forerunners looked like and when, where, and how they evolved, but also specifically asks, for example, why humans evolved while other primate species died out (White 1988; Tattersall and Schwartz 2000). We have to reconstruct the ecological niches of fossil humans to define the determinants that caused adaptation in human evolution, a process sometimes defined as hominization, although some anthropologists argue that this term is misleading as it sounds teleological (Delisle 2001). Hence, when using this concept, we should be aware that it describes a teleonomic process sensu Pittendrigh (1958). In paleoanthropology – as in other life sciences with a chronological perspective – the experiment is in the historical process of nature itself. We have correspondingly to interpret this process within the general principles of evolutionary theory ex post-factum, and we have to take into account all the problems that arise from the epistemological difficulty known as subject-object identity (Riedl 1975; Mahner and Bunge 2000; Vogel 2000; Vollmer 2003).

Why a Scientific Historical Approach to Paleoanthropology?

The present review of the historical development of paleoanthropology as a multifaceted biological subject is intended to focus on its cultural and social background and on its many problematic time-specific aspects. This historical point of view promises to clarify the following questions:

- Which paradigmatic changes in evolutionary thinking have guided the field of paleoanthropological research?
- Which cultural, social, and scientific factors have decelerated or accelerated the progress of paleoanthropology?
- Which outstanding scientists, and which ideas, brought about the integration of biological, geological, and archaeological research?
- What underlies the successive development, respectively, from Darwinism to neo-Darwinism and from the Synthetic Theory and “Modern Synthesis” to the

System Theory of Evolution as the concept and strategy of paleoanthropological research?
- What were country-specific impacts on the orientation of paleoanthropological research?
- What influence of political ideologies and systems (e.g., radical authoritarian nationalism, communism, colonialism) can be noted on paleoanthropological thoughts and research?
- How was paleoanthropological thought on sex-specific roles in human evolution influenced by the fact that this subdiscipline was for long male dominated?
- What is the impact on current paleoanthropology and its image of innovative biological techniques in these multimedia times?
- Is paleoanthropology a fossil- and/or media-driven science, triggered by the discovery of and publicity about exceptional hominin fossils?
- If the accusation is correct that paleoanthropologists offer mainly shallow but media-friendly "findings" (White 2000) that contribute only very little to a proper understanding of the pattern and process of human evolution (following Shakespeare: "Much Ado About Nothing"), how can historic studies on paleoanthropology contribute to new educational strategies to survive antievolutionary thinking?

Paradigmatic Change in the Nineteenth Century: Step by Step

Darwin's Forerunners, Especially in France and England

The biblical view of the permanence of species expressed by Linnaeus' sentence "*Species tot sunt diversae*, *quot diversas formas ab initio creavit infinitum ens*" was the underlying dogma of Genesis and the Judeo-Christian tradition. Although animal fossils had been described long before Darwin's theory was published, they were interpreted as witnesses of "lost worlds" within cataclysm models, and not as evidence of a real historical-genetic process (for contemporary views, see, e.g., Paley 1860; Zöckler 1860, 1876; for recent literature on pre-Darwinian thinking, see, e.g., Nebelsick 1985; Corbey and Theunissen 1995; Livingstone 2008; Bayertz 2012; Schwarz 2012; Ingensiep 2013).

Georges Cuvier (1769–1832), the outstanding French comparative anatomist, did pioneering research on mammalian fossils and contributed to the self-consciously new science of geology. He began to understand that fossils truly represent remains of once-living organisms and argued for the reality of extinction caused by sudden physical events, so-called catastrophes. Cuvier first opened up the geohistorical perspective that is now appreciated as his most important legacy to science (Rudwick 1997). Besides this, he adamantly rejected "transformist" explanations. Although he was doubly on the wrong track, and his remark "*l'homme fossile n'existe pas*" slowed the development of thinking on human evolution, Rudwick's interpretation of the primary texts demystified Cuvier, who was one of the first to professionally plan his research. His approach had an important influence on scientists of his time.

One of the outstanding opponents of catastrophism was Sir Charles Lyell (1797–1875), British geologist and popularizer of uniformitarianism. He defended one of the most basic principles of modern geology, the belief that fundamentally the same geological processes that operated in the distant past also operate today. *Principles of Geology*, his specific work in the field of stratigraphy, was the most influential geological work of the middle of the nineteenth century and did much to put geology on a modern footing (Bynum 1984; Wilson 1998).

In spite of much progress in natural scientific thinking, the early explanatory approaches of evolutionary theorists were not able to replace traditional views. All pre-Darwinian explanations of diversity and variability are regarded as just another story of natural history, because they failed to explain the driving force of evolution. This holds true for such outstanding naturalists of the eighteenth century as Georges-Louis Leclec, Comte de Buffon (1707–1788); Erasmus Darwin (1731–1802), grandfather of Charles R. Darwin; and William Paley (1743–1805), whose *Natural Theology*, *or Evidences of the Existence and Attributes of the Deity Collected from the Appearances of Nature* was a best seller of which the 20th edition was published in 1820. Paley tried to prove that the world has been created by a designer. Charles Darwin had studied Paley's "long argumentations" carefully, as he noted in his *Autobiography*, before he wrote "I think" in his *First Notebook on Transmutation of Species* (1837) (for concise information on the dispute between theology and natural sciences during the last four centuries, see Schwarz 2012).

The evolutionary theory of Jean Baptiste de Lamarck (1744–1829) proved to be a nonvalid explanation for transformation. However, Charles Darwin (1809–1882) looked upon this retrospectively as an "eminent service of arousing attention to the probability of all changes in the organic, as well as in the inorganic world, being the result of law, and not of miraculous interposition" (Darwin 1861, preface). For a revised assessment of Lamarck's merits, see Wuketits (2009a).

Lamarck's theory triggered Darwin's evolutionary thinking on "transmutation" of species; Darwin himself regarded his Lamarckianistic *pangenesis theory* in retrospect as "stillbirth" (see Wuketits 2009b, p. 626). However, it was foremost Lyell's *Principles of Geology* and Thomas Malthus' essay on the *Principle of Population* (which stated that the population size is limited by the food resources available) that inspired Darwin to his multifaceted approach toward deciphering the biological principles of evolution. He defined the fundamentals and described evolution as a self-organizing process by a mutation-selection mechanism without the necessity of a creator or deus ex machina. The driving force of this event, natural selection (codiscovered by Alfred Russell Wallace, 1823–1913), is the central explanation of the evolutionary process (Glaubrecht 2008a, b).

Darwin's and Wallace's legacy, the theory of natural selection, ultimately led to a paradigmatic change, a totally new view of the development of life systems including human origins. The vintage philosophical questions "Who are we?" "Where do we come from?" and "Where are we going?" were transferred from the metaphysical and the philosophical to a biological focus. They created new and important existential questions. Kuhn (1962) saw the truly revolutionary aspect of

Darwin's theory, not as lying in its evolutionism, but in its powerful rejection of the traditional, teleological view of nature. How explosive Darwin's evolutionary theory was, and how conscious Darwin was of this, is reflected in the fact that he hesitated to deal with the questions of human evolution. The first edition of his classical opus *On the Origin of Species by Means of Natural Selection*, or *the Preservation of Favoured Races in the Struggle for Life* (Darwin 1859), provides proof of this feeling of insecurity. It then took him 12 years to publish his ideas in *The Descent of Man and Selection in Relation to Sex* (Darwin 1871). His innovative focus on human origins set the context for many of the themes of paleoanthropology during the following century. The anthropological challenge within the dynamic evolutionary concept was how to explain ourselves without compromising our posture. Altner (1981a, p. 3) verbalizes the existential problem as follows: "*Der neuzeitliche Mensch ist aus allen ihn übergreifenden Sinnbezügen herausgefallen und auf sich selbst und sein Werden zurückgeworfen*." (For more recent literature on the impact of Darwinism to contemporary and current philosophical thoughts, see Becker et al. 2009; Bohlken and Thies 2009; Engels 2009.)

Evolutionary thinking was widespread during the nineteenth century as various science historians have shown. Bowler (1988, p. 5) suggests in this context "that Darwin's theory should be seen not as the central theme in the nineteenth-century evolutionism but as a catalyst that helped to bring about the transition to an evolutionary viewpoint within an essentially non-Darwinian conceptual framework."

Nowadays we know that most late nineteenth-century evolutionism was non-Darwinian as "it succeeded in preserving and modernizing the old teleological view of things"; however, it was a revolution "in the sense that it required the rejection of certain key aspects of creationism," as Bowler (1988, p. 5) says (see also Moore 1981; Desmond and Moore 1991). The heart of Darwin's materialism, the theory of natural selection, had little impact until the twentieth century. For this reason, the Darwinian Revolution did not take place in the second half of the nineteenth century and remained incomplete until the synthesis with genetics in the twenties and thirties of the last century. But even after this breakthrough, there was no straightforward scientific approach in paleoanthropology until anthropologists appreciated the essential corollary of Darwin's theory, that we are only "another unique species" (Foley 1987).

In retrospect it becomes obvious that the earliest "evidence" for human evolution was disregarded and misinterpreted. Fossils do not speak, but the dictum in paleontology is that they give silent witness. One can only get morphological, ecological, or taxonomical information within a concise methodological approach. Apparently easy paleoanthropological questions about the space and place of human origins do not necessarily have easy answers, so it requires rigorous efforts to establish a sophisticated research design and an adequate methodology to find solutions for the key questions given earlier (see section on "Why a Scientific Historical Approach to Paleoanthropology?").

As there was no evolutionary context at the time when William Buckland (1784–1856), professor at the University of Oxford, discovered the first human fossil, the "Red Lady of Paviland" at Goat's Hole in South Wales in 1823, he totally misinterpreted this 26-ka-old find (Sommer 2004, 2006, 2007a). Buckland considered the find as of postdiluvian age and was unwilling to attribute any great antiquity to this Upper Paleolithic fossil skeleton.

"For most of the nineteenth century, no one believed or anticipated discoveries that would demonstrate a history of humans and their ancestors stretching back over more than a few thousand years," wrote Trinkaus and Shipman (1993, p. 9). Although savants struggled with evolutionary ideas for decades, the belief persisted that the human past differed from the present only in the "primitiveness" of the ancient peoples, not in their very essence and being. Starting in the twenties of the nineteenth century, there sprang up one local natural history society after another. The Red Lady inspired the hunt for human fossils and artifacts (Sommer 2004, 2006, 2007a; Delisle 2007). Kent's Cavern in Torquay, Devon, today recognized as one of the most important archaeological sites in the British Isles, was excavated by John MacEnery and William Pengelly (1812–1894) (Sackett 2000). They discovered an Upper Paleolithic skeleton in association with flaked stone tools. John Lubbock (1834–1913), the foremost British archaeologist at that time, refused the report on "modern savages" written by Godwin-Austin and considered the findings as "improbable" (Trinkaus and Shipman 1993). Lubbock divided the Stone Age into two distinct periods, the Paleolithic and the Neolithic, based on the presence of crudely shipped flint tools versus more subtly made tools. Goodrum (2009, p. 341) mentions Lubbock's *Prehistoric Times* (1865) and Daniel Wilson's (1816–1892) work on *Prehistoric Man* (1865) as landmark in "the emergence of a new discipline, prehistoric archaeology, and the use of the term 'prehistory' in English" (overviews in Sackett 2000; Goodrum 2009, 2013).

Phillipe-Charles Schmerling (1791–1836), a Belgian physician and anatomist, unearthed an infant skull in 1829/1830 at Engis near Liège, which was diagnosed later as a Neanderthal fossil. The Engis child was the first specimen of this kind to be discovered (Schmerling 1833). During the same period, Casimir Picard (1806–1841), a physician and avid archaeologist, was excavating prehistoric stone tools in France. His passion was in taking an experimental approach to archaeology, and he attempted to make and use stone artifacts like those that were being found in excavations. Due to inadequate chronology of the artifact-bearing horizons, he was not able to calibrate some of his stone tools as Neolithic. But his experiments led him to conclusions about how the tools were manufactured. Picard developed, for the first time, both systematic excavation techniques and a stratigraphic approach. While his innovative research was without wider impact on archaeological progress, he impressed his friend Boucher de Perthes (1788–1868). This influential aristocrat, who combined his romantic views on human origins with archaeological fieldwork, argued for the existence of Pleistocene – or, as he said, pre-Celtic-humans; but his findings were at first disregarded by the scientific community. When, in 1864, some of his findings were published in *The Anthropological Review*, the comment of the scientific board was downright British: “We abstain at the present from offering any comment on the above” (Trinkaus and Shipman 1993, p. 44). Although Boucher de Perthes could not avoid the image of flamboyant enthusiast and “madman,” there was finally a change in the assessment of the hand axes as genuine tools. The careful excavation of the gravel beds of the Somme at St Acheul by the French amateur naturalist Marcel-Jérôme Rigollot (1786–1854) impressed a group of outstanding British colleagues, among them Charles Lyell (Fritzsche 1997), and led to the acceptance of the claim that the hand axes were associated with extinct mammal bones – but where did this leave the human fossils? (See Klein and Edgar 2002; Goodrum 2009; Wuketits 2009a)

Neanderthal Case: “Neanderthals Without Honor”

The Neanderthal man from the Kleine Feldhofer Grotte in the Neander Valley near Düsseldorf was found by limestone workers in 1856 and described by the local teacher Johann Carl Fuhlrott (1803–1877). The fossil was the first early human specimen to be recognized as such. The discoveries from Engis (found 1829) and Gibraltar (found before 1848) were made sooner, but their nature became evident much later. Fuhlrott’s merit was that he realized the significance of the fossils, which the limestone workers took for animal bones. Luckily, the owner of the excavation site saved them at the last moment (Schmitz and Thissen 2000). Fuhlrott fought, together with the anatomist Hermann Schaaffhausen (1816–1893) who taught at the University of Bonn, for their acceptance as ancient remains from the diluvial age. Both were convinced that the morphological structure of the bones indicated a high-diluvial age. Since the discovery of the fossil bones antedated the publication of Darwin’s *Origin of Species*, this specimen has often been termed as first proof for human evolution. A deeper analysis of the Fuhlrott/Schaaffhausen contribution demonstrates that both protagonists of paleoanthropological research in Germany were far from an evolutionary interpretation, although they looked upon their fossils as diluvial forerunner of recent *Homo sapiens* (Zängl-Kumpf 1990).

A contemporary of Fuhlrott and Schaaffhausen was Thomas Henry Huxley (1825–1895), the famous British zoologist often referred to as “Darwin’s Bulldog” (Desmond 1997). However, Huxley was no Darwinian. Historians know the difficulties of accurate definition, and Hull (1985, 1988) gets to the heart of this problem in suggesting “that Darwinians are simply those scientists who expressed loyalty to Darwin as the founder of evolutionism, whatever their beliefs about how evolution actually works” (Bowler 1988, p. 73). Although Huxley was highly committed by Darwin’s theory, it is well known that he had essential problems with the selection theory. Further, he was strongly tempted by non-Darwinian ideas, e.g., internal factors that would produce changes independent of the environment. Not being really interested in adaptation, Huxley speculated that evolution might sometimes work in a saltatory manner (Bowler 1988; Desmond 1997). His position was that the continuity between humans and other animals does not detract from the inherent specialness of humans. Similarly, other contemporary so-called proponents of Darwinism were not at all Darwinian evolutionists. In his famous papers on *Evidences as to Man's Place in Nature*, Huxley (1863) gave morphological arguments for our relationship with recent primates and pointed to the scant fossil record known in his time. In spite of contrary statements by many historians, Huxley said virtually nothing about human origins, but concentrated exclusively on demonstrating the physical resemblances of humans and apes. Concerning the Neanderthal man from Germany, Huxley conducted a sophisticated comparison with anatomically modern skulls from Australian Aborigines and other aboriginal relicts, pioneering new ways of orienting and measuring skulls for easier comparison (Desmond 1997). His conclusion was that the Neanderthal skull emerged as an exaggerated modification of the lowest of the Australian skulls. Huxley stated that the brain of the Neanderthal man was of normal size for an ancient savage, and its stout limbs suggested to him a cold adaptation to glacial Europe. However, in no sense was this specimen "intermediate between man and apes." He viewed the Neanderthals as a very "primitive race" of humans, "the most pithecoid of human crania yet discovered" (Huxley 1863, p. 205). The Huxley biographer Desmond (1997) illustrates this by reference to Huxley's diary entries: "Where, then must we look for primeval Man? Was the oldest *Homo sapiens* pliocene or miocene, or yet more 'ancient'? How much further back must we go to find the 'fossilized bones of an ape more anthropoid, or a man more pithekoid' (sic!)?" Desmond concludes that Huxley was preparing the world for ancient semihumans. How misleading the effects of the concept of "semihumans" were becomes evident from the popular scientific literature and illustrations (see Corbey and Theunissen 1995; Kort and Hollein 2009, herein especially Jane Goodall's article; Ingensiep 2013).

The Irish zoologist William King (1809–1886) proposed in 1864 the name *Homo neanderthalensis*, although his arguments for a separate species in the genus *Homo* were inadequate, not to say absurd. Since then, opinion has fluctuated as to whether the fossils should be considered as a separate species, *H. neanderthalensis* or *H. sapiens neanderthalensis* (a subspecies of *H. sapiens*). The "fate of the Neanderthals" is the trickiest controversy in paleoanthropology (e.g., Henke and Rothe 1999b; Stringer and Gamble 1993; Tattersall 1999; Krings et al. 1997; Wolpoff 1999; Henke 2003a, b, 2005; Finlayson 2004; Green et al. 2008, Green et al. 2010a, b; Condemi and Weniger 2011; Stringer 2012). The question of whether some or all of these fossils deserve a place in our direct ancestry or whether they can be viewed as a single lineage leading to and culminating in the classic Neanderthals of the last Ice Age is the longest-running taxonomic problem in paleoanthropology (Schmitz 2006; Uelsberg and Lötters 2006; Harvati and Harrison 2006; Cartmill and Smith 2009). What very soon became apparent with Huxley's *Evidences* was the tremendous need for an extension of the fossil record and for an improved comparative methodology to analyze and interpret the fossils of recent primates. The starting signal for the search of the so-called missing link was given.

Theoretical and Methodological Progress in Paleoanthropology Since Darwin Till Mid-twentieth Century

Successive Discovery of the Paleoanthropological Background

In Darwin's time, it was already evident that the scant evidence of hominin life in the past does not allow us to neglect any clues. We need all available sources to reconstruct our evolutionary history, and to do this we rely overwhelmingly on fossils. No wonder the mantra of paleoanthropologist's of the first hour was "We Need More Fossils!" – and this call has never faded. However, there arose a paradox: the more fossils, the more complex the phylogenetic interpretations of the material became. Begun (2004) even wondered "Is Less More?" The answer must be an improvement of the epistemological and methodological bases of paleoanthropological inquiry, to ensure the trustworthiness of the investigation of fossils. These latter are obviously mute; and for this reason, one has to formulate hypotheses about the biological and phylogenetic roles of the extinct taxa. The only reliable approach to increasing our knowledge of the lost worlds is to compare them with recent sets of well-known phenomena (Foley 1987; Henke and Rothe 1994).

This scientific process started very soon after the creative flash (fulguration sensu Popper) of the pre-Darwinian interpretation of fossil specimens as documents of species of former times and of their relevance to Darwin's evolutionary theory. It was in this context that the systematic search for phylogenetic forerunners of recent taxa began. The most dramatic part of the Darwinian paradigm focused on the question of how humans evolved from archaic primates. What did the hypothetical species transitional between apes and man look like? When, where, and how did the "missing link" live? (The origin of this term is contested. Some claim it was created in 1861 by Asa Gray (Shipman and Storm 2002), while other sources say it was coined by Lyell in 1837). Like the term "semihumans," just mentioned, this concept caused a lot of misunderstandings (Goodall 2009; Ingensiep 2013), and for this reason it should be abandoned as inadequate for modern evolutionary thinking. However, John Reader's (2011) *Missing Links*, an enthralling story of fossil hunting, stuffed with eccentrics and enthusiasts, and even some frauds in the search for humanity's origins, demonstrates the hold this expression has had on the popular scientific media since Herbert Wendt's (1953) best seller *Ich suchte Adam*. Fortunately, controversial book titles don't implicitly match with a book's contents; reader's advanced and ambitious storytelling is as diverting as Wendt's publication which first aroused my interest in the subject. Darwin's evolutionary theory of natural selection did not automatically provide an answer to the question of human ancestors, and Darwin himself was cautious enough not to give a premature answer. But he had provided a new framework in which all these questions could be answered. While the public longed for strong proof of human evolution, Darwin gathered all available arguments for more than 10 years before finally publishing his brilliant anthropological volumes *The Descent of Man and Selection in Relation to Sex* (1871) and *The Expression of Emotions in Animals* *and Man* (1872). Both books deal with human evolution, and particularly with sexual selection, whose enormous evolutionary impact was first understood only around 100 years later, when the sociobiological paradigm emerged (Wilson 1975; Vogel 1982; Miller 1998; Voland and Grammer 2002; Voland 2000a; 2009).

During the 1860s, Darwin's ideas were widely popularized. However, there was still much scientific skepticism since the laws of heredity worked out by Gregor Mendel (1822–1884) in 1865 remained unknown until the twentieth century. Beside Darwin's British supporters, especially Thomas H. Huxley and Charles Lyell, it was the German geologist and paleontologist Friedrich Rolle (1827–1887) and the zoologist Carl Vogt (1817–1895) who advocated Darwin's theory (Rolle 1863; Vogt 1863; for more details, see Bowler 1988; Junker and Hoßfeld 2002; Hoßfeld 2005a, b; Rupke 2005; Ruse 2005).

Even more committed and sarcastic than the "Affenvogt" was Ernst Haeckel (1834–1919), an outstanding German biologist who sagaciously fought against the "ape complex." He is best known for his *recapitulation law* (ontogeny recapitulates phylogeny), a highly controversial assumption. After reading *The Origin*, he became a powerful and eloquent supporter of evolution. Although Haeckel admired Darwin's theory, he remained an orthogradualist and a Lamarckian concerning the concept of the "survival of the fittest." Haeckel was not really supportive of natural selection as the basic principle of evolution, and his interest in fossils and paleoanthropology was small. He was convinced that due to the intertwining of phylogeny and ontogeny, ontogenetic structures were sufficient evidence for evolution (Haeckel 1898, 1902, 1905, 1922; Heberer 1965b, 1968b, 1981; Hoßfeld and Breidbach 2005; Kleeberg see www; Preuß et al. 2006; Henke und Rothe 2006; Sarasin and Sommer 2010).

Despite misunderstanding many of Darwin's ideas, Haeckel inspired the public and colleagues with his enthusiasm for evolution and animated the debate. As he was highly motivated by his anti-Christian attitude, his influence in science faded, especially after he had created his monistic theories and dabbled in esoteric fields (Hoßfeld 2005b; Kleeberg see www; Richards 2005). Still, he gave paleoanthropology an essential impulse by publishing the first phylogenetic tree (Fig. 4) that included humankind. Darwin's comment on this was "Your boldness, however, sometimes make me tremble, but as Huxley remarked, some one must be bold enough to make the beginning in drawing up tables of descent" (German translation "Ihre Kühnheit läßt mich jedoch zuweilen erbeben, aber, wie Huxley bemerkte, irgend jemand muß eben kühn genug sein und einen Anfang machen, indem er Stammbäume entwirft") (Darwin's letter to Haeckel, November 12, 1868) (Schmitz 1982). As the limited fossil record only allowed a very hypothetical pedigree, there was much courage needed indeed. Haeckel postulated a forerunner species *Pithecanthropus alalus* – a speechless ape-man – a missing link, which he believed lived during the Pliocene in Southeast Asia or Africa. Within an orthogenetic pedigree, he posited a primitive species – which he named *Homo stupidus* – between this "ape-man" and the recent *H. sapiens*. Around 30 years later, fossils were found

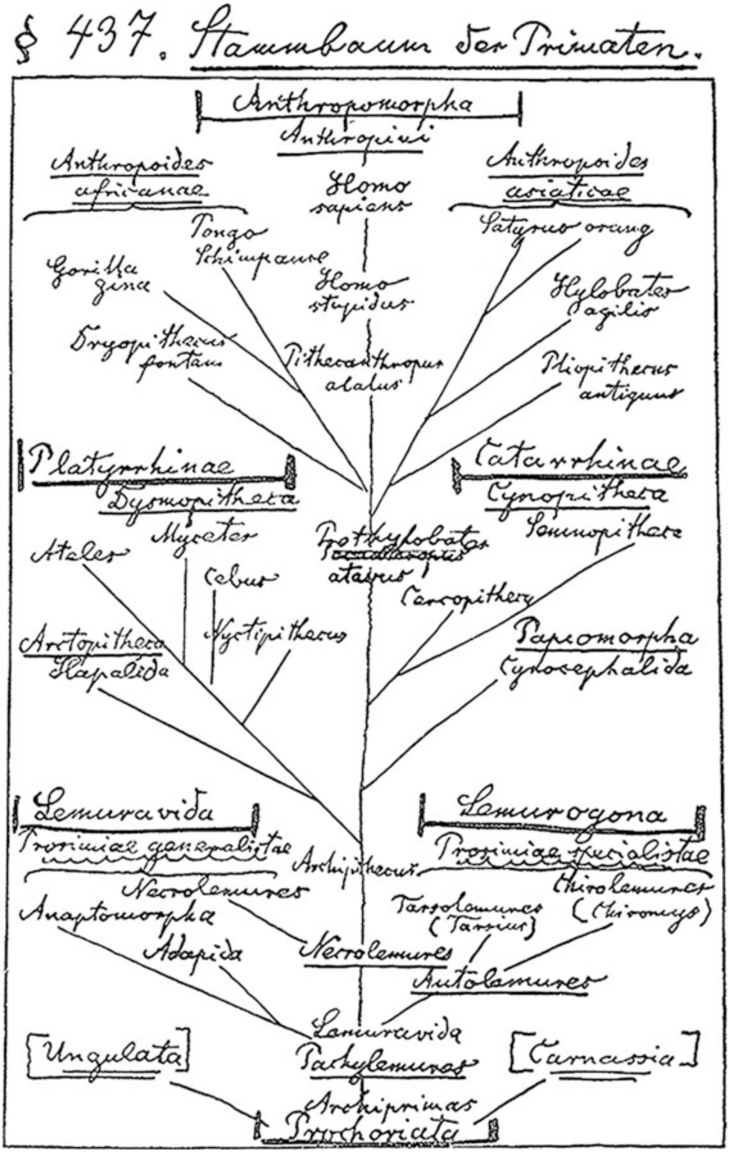


Fig. 4 Hand-drawn sketch of the family tree of primates by Ernst Haeckel; published in Herbert Wendt: *Ich suchte Adam*, 2nd ed. 1954 (Grote Verlag, Hamm). The artwork is part of the estate of Gerhard Heberer, and currently in the possession of Uwe Hoßfeld (Jena). Due to a detailed recherche by David Morrison (see Morrison et al. (2013), www), it was detected that contrary to earlier claims, this is *not* the first primate pedigree from Haeckel; there is evidence to suppose that the sketch was designed around 1895

in the postulated Asian region by the Dutch physician Eugene Dubois (1858–1940), which roughly fitted the expectation of a *Pithecanthropus* (Bergner 1965).

Meanwhile a focus of research was the phenomenon of the Ice Ages and the discovery of Upper Paleolithic man and Ice Age cultures (Trinkaus and Shipman 1993; Sackett 2000). Although human fossils were rare at the time of Darwin's revolutionary discovery, there was much evidence from animal bones, mollusks, sediments, and other materials to give insight into ancient populations. Further, there were ever-increasing indications of long-term fluctuations in the earth's climate. Geologists, like Agassiz, Geike, and Lyell as well as Brückner and Penck, established a Pleistocene framework of successive glaciations (Gräslund 1987), and archaeologists strove to establish the antiquity of human ancestry through the association of stone tools with extinct animals. The geological research resulted in the Alpine model, a chronological system of glaciations that gave a framework for the ongoing discovery of Neanderthal fossils.

As biological, anthropological, paleontological, geological, and archaeological data came together within the framework of the evolutionary theory during the second half of the nineteenth century, many scientific societies were founded, which supported all kinds of scientific research.

Rudolf L.C. Virchow (1821–1902), a famous German physician and anthropologist sensu lato, best known for his guiding research in cellular pathology and comparative pathology, was a universal scientist and liberal politician who founded the German Society of Anthropology, Ethnology, and Prehistory in 1869 (Degen 1968; Andree 1976; Schipperges 1994; Goschler 2002; Saherwala 2002; Trümper 2004). He included humankind in the historicization of nature and came to the conclusion that *H. sapiens* was "post-history" (Goschler 2002, p. 322). For that reason, he was highly skeptical about the validity of Darwinian theory as regards our own species and doubted the phylogenetic classification of the species *H. neanderthalensis*, as the Irish zoologist William King had dubbed the skeleton from the Kleine Feldhofer Grotte (Stringer and Gamble 1993; Trinkaus and Shipman 1993; Schmitz and Thissen 2000). Due to his "pathologist view," he interpreted the Neanderthals' derived features, or apomorphies, as pathological features resulting from arthritis; further, from the erroneous information that the skeletal remains were associated with polished stone tools (an indicator for the Neolithic), he concluded that the Neanderthal specimen must have lived in recent times (Schott 1979). Thus, not all human fossils known at that time were accepted as convincing evidence of our ancestry, especially given their uncertain dating.

Neither Virchow nor Haeckel pushed paleoanthropological research, the former from misinterpretation of the facts and skepticism on Darwin, the latter from his conviction that ontogenetic research delivers sufficient information to demonstrate phylogenetic evolution. Virchow's interest was much more in prehistoric anthropology and ethnology, from the point of view of the decoupling of natural and cultural evolution. The retrograde view that the assumed "missing link" does not exist was admired by the Christian church, and when *Pithecanthropus erectus*, the so-called Java man, was described, he thought that the bones represented a giant gibbon. However, Haeckel's interpretation was not in accordance with the results of the discoverer. Dubois was convinced “that his famous specimens from Trinil represented a true human ancestor, while other fossils from Sangiran and Zhoukoudian in China were too derived to have been ancestral to later humans. His theories, however, were widely misunderstood at the time” (Durband 2009, p. 10). As an excellent proof that in science history really matters, it can be noted that his “somewhat bizarre” reading of the evidence was roundly chastised by anatomists of the time (e.g., Le Gros Clark 1934; Weidenreich 1946) and generally dismissed by the scientific community as a whole. Only decades later, through the efforts of Theunissen (1989) and later Shipman (2001), were Dubois’ motives for this stance made clear (Durband 2009, p. 10; see too Theunissen 1989; and Shipman 2001).

Virchow’s skeptical attitude concerning *Pithecanthropus* as well as his critical interpretation of the Neanderthal fossil as a pathological individual lessened the biological impact of a premature “paleoanthropology” in Germany during the second half of the nineteenth century (Trümper 2004). This holds true for the English and French scientific scenes as well. Although the physician Paul Pierre Broca (1824–1880), the founder of the Société d’Anthropologie de Paris in 1859, was a pioneer of comparative anatomy and anthropology, he never accepted the Neanderthals as fossil documents. His interest was in understanding patterns of variation in order to understand the significance of anatomical differences. For this reason, he became one of the first to use statistical concepts in establishing anthropology as a scientific discipline in contrast to medical science. In 1882, his French colleagues Quatrefages and Hamy published *Crania ethnica*, a monograph which exemplifies the huge interest in recent cranial variation that dominated the anthropological discipline.

Édouard Lartet (1801–1871) was the first to describe the primate genera *Dryopithecus* and *Pliopithecus*, but much more important was his discovery of signs of prehistoric art made by early humans (Lartet and Christy 1865–1875). The fossil ivory carving of La Madeleine, found in 1864, was presented at the world exhibition in Paris 1867 and raised tremendous interest.

In the following period, neither the discoveries of human fossils from La Naulette in Belgium nor those of Pontnewydd (Wales), Rievaulx (Southern France), Šipka, Mladeč (see Teschler-Nicola 2006), and Brno (Čzech Republic) were able to convince the European scientific community of great human antiquity. Even the analysis of the Spy fossils, which had been discovered in Belgium in 1886, did not slow the rejection of evolutionary ideas. Trinkaus and Shipman (1993, p. 132) summarized: “The man of the Neander Valley remained without honour, even in his own country.”

In the motherlands of evolutionary thinking, France and England, Paleolithic archaeology dominated paleoanthropological discussion as it began taking shape as an organized scientific field of research in the 1860s. Sackett (2000, p. 38) put it this way: “discovering the Paleolithic became a matter of empirically demonstrating that human remains and artifacts could be found in association with the remains of extinct animals belonging to the deep time of earth history.”

Progress was for the first time possible through the geological recognition of the Pleistocene epoch, making the interpretation of fossils possible within a solid geological background. Although Cuvier and Lyell had done indispensable scientific work in understanding the past, the first assumed that the changes came about by a series of revolutions, while the second, although he had major objections to Cuvier's theory of catastrophism, was no evolutionist either. The challenging question for the evolutionists was how to provide empirical data on the existence of "diluvial" and "antediluvial" early human populations. As these workers had to rely on the research of the paleontologists and the archaeologists, paleoanthropological science was becoming multidisciplinary even at this early stage. The evidence from the Paleolithic record was mainly from data from stream gravel terraces, rock shelters, and bone caves. As Sackett (2000, p. 42) mentions, from the 1820s until 1859, there was a series of discoveries in France (especially in the Perigord), England (Paviland bone cave near Swansea, Wales; Kent's Cavern, near Torquay, Devonshire), and Belgium (Engis near Liège). The research resulted in the assignment of Pleistocene faunas to deep geological times, but it did not support evolutionary thinking due to the many alternative explanations available. The consequent question was whether actual human remains existed in association with Pleistocene animal fossils and undoubted artifacts. The immediate question of human antiquity came up with the discussion of the fossils from the Neanderthal in Germany and Darwin's evolutionary theory. Most of the geologists and paleontologists remained skeptical; they saw no proof of a high antiquity of humankind from evidence from the bone caves or gravel terraces. One reason for their skepticism resulted from the archaeological work of Jacques Boucher de Perthes, director of customs at Abbeville, France, whose empirical evidence was much doubted. As consequence of his having "found much too much," as Sackett (2000, p. 45) put it, the Bible continued to dominate everyday metaphor; and ironically enough, the successful archaeological research in the Near East, Egypt, and Palestine solidified the traditional view that humankind was unique and doubtless recent. In spite of many convincing facts – as retrospectively gauged – from archaeology, the social establishment of the mid-nineteenth century maintained the older view.

An opportunity for change came in 1858, when Brixham Cave near Torquay on the Devon Coast was discovered, and outstanding scientists like Hugh Falconer (1808–1865), Charles Lyell, Richard Owen (1804–1892) supervised excavations there. William Pengelly (1812–1894), a local schoolteacher and geologist, was able to gather, by a new method of layer-by-layer excavation, thousands of animal bones including those of hyena, cave bear, rhinoceros, and reindeer. The impact of these fossils on the question of human antiquity would have been zero if Pengelly had not found undeniable artifacts, which he described as "knives." These chipped stones from Brixham Cave challenged the received opinion about human antiquity in 1859. While the belief in human antiquity of the excavator and some colleagues was confirmed by the association of fossil bones and the hand axes, others like Owen did not agree and thought that the animals had not become extinct until geologically modern times.

New aspects came into the stagnating discussion when the implements of the Brixham Cave were compared to the finds at Abbeville and Amiens excavated by Boucher de Perthes. The ultimate convincing facts came when the English team, digging in the Somme terraces, was able to document a hand axe in place in a fossil-bearing stratum at St Acheul. This was the turning point as Pengelly, Prestwich, and Lyell were then able to convince the British establishment of the antiquity of humankind. The French scientific community, which had contradicted Boucher de Perthes' interpretations for many years, now no longer rejected the idea of human antiquity. Some French scientists like the zoologist Isodore Geoffrey St Hilaire (1805–1861) and Édouard Lartet had been more or less convinced about human antiquity before, but the discovery of human teeth intermixed with fossils of cave bear and hyena in a cave near Massat in southern France brought about final acceptance. Lartet published the ultimate proof in 1860. He described cut marks on fossil bones that had been made by stone tools when the bones were still fresh. This was the essential evidence of contemporaneity of humans and extinct animals, and it signaled the start of intensified geological research. The glaciological research aimed at structuring the Pleistocene epoch that helped to put the human antiquity into a chronological frame; and the amalgamation of archaeological and geological facts brought up a new era that started with Lyell's first edition of his famous *Geological Evidences for the Antiquity of Man* (Lyell 1863). The coming together of diverse aspects of the cultural and natural sciences ultimately yielded an innovative conception of man and his origin (Daniel 1959, 1975; Trinkaus and Shipman 1993; Sackett 2000; Murray 2001; Sommer 2004, 2007a; Delisle 2007).

Southeast Asia as Supposed Cradle of Humankind

If paleoanthropologists had to answer the question of which fossils had the most exceptional influence on human evolutionary thinking, they would, of course, include the *Homo erectus* fossils from Java alongside those from the Neander Valley (Theunissen 1989; Durband 2009). The assessment is very easy to understand: first, there is a hero, a young, enthusiastic physician from the Netherlands, Eugène Dubois, who feels inspired by Darwin's theory and Haeckel's preliminary draft of a link between the lesser apes and earliest human populations; he joins the army as military surgeon and embarks for Indonesia. Besides his service in the army, he is looking for the so-called missing link, *P. alalus*, as Haeckel had dubbed the speechless and small-brained human species (Shipman 2001; Shipman and Storm 2002). Second, this paleontological amateur is successful in discovering a fossil human tooth and then a skullcap in the gravels of the Solo River. He proposes at first the name *Anthropopithecus* and then changes it to *Pithecanthropus*, the name given by Haeckel. Finally, a stroke of good fortune leads to the discovery of a human femur, which seems to belong to the *Pithecanthropus* fossils, and causes the species to be named *erectus*. Third, Dubois, the man who found the posited "missing link," gets into more and more trouble with his critics and, due to severe personal problems, the end of his career is tragic. Since Dubois was neither an accidental discoverer nor a paranoid eccentric person, as science historians and colleagues (v. Koenigswald 1971) have sometimes characterized him, the reinvestigation of his lifework yields a less discreditable view (Theunissen 1989; Shipman 2001; Shipman and Storm 2002; Durband 2009).

If one takes all aspects of this story together, it shows the main characteristics of a myth. On the one hand, his unbelievable luck and, on the other hand, his unyielding, difficult character and his stubborn nature made Dubois an interesting public figure. While some historians like Erickson (1976) look upon Dubois as an unimportant figure in paleoanthropology, others like Haddon (1910), Theunissen (1989), and Shipman (2001) see him as one of the founding fathers of paleoanthropology (Shipman and Storm 2002).

Did Dubois' essential discovery coincide with a paradigm shift in paleoanthropology? While Howell (1996, p. 4) stated that the entire field of paleoanthropology is "close to a paradigm state without yet having achieved it," Chamberlain and Hartwig (1999, p. 42) suggest "that the validity and promotion of knowledge claims in palaeoanthropology are explicitly Kuhnian and that future epistemological progress depends on acceptance of both Kuhnian and positivist approaches to knowledge-building."

In opposition to Chamberlain and Hartwig's opinion, Cartmill (1999, p. 46) stated that "Whatever a paradigm is, normal science consists of attempts to 'articulate' a paradigm by answering questions, verifying predictions, and solving sticky problems in paradigmatic terms." He continues: "Conceptual change in science is perpetually going on at all levels, and is not ordinarily concentrated in punctuational events that can be distinguished as 'revolutions'."

Whatever position one adopts, there are obviously good reasons to regard Dubois as a founder of paleoanthropology. According to Shipman and Storm (2002, p. 109), founders must have special qualifications, e.g.:

- A pivotal discovery of fossils or artifacts
- Development of an innovative technique for the description and analysis of discoveries
- A new framing of the problems or questions of the fledgling field
- A broad dissemination of information or debate about the subject, which serves to make it a matter of wide concern
- The provocation of a general reaction or response from potential colleagues

The last point fits with the Machiavellian fact that an invention needs the attention of the scientific community to become common currency. One may ask what would have happened to Dubois' discovery in modern times. The rules of "The Economy of Attention," formulated by Georg Franck (1998a, b), list the following stepwise pattern: "Attention by other people is the most irresistible of drugs. To receive it outshines receiving any other kind of income. This is why glory surpasses power and why wealth is overshadowed by prominence."

While Haeckel, Broca, and other scientists focused on the comparative anatomy and embryology as proof of human evolution, Dubois was the first who implemented a new strategy. Since he realized that human evolution is a chronological process, which must have happened in preferred localities with specific ecological niches, he set out for Southeast Asia, promised by Haeckel's fictional pedigrees as a possible "cradle of mankind" where the mysterious so-called missing link should have lived.

Dubois was the first to write a detailed monograph on a hominin fossil, and he applied for the first time metrical and mathematical procedures for the calculation of brain volumes and stature heights to a human fossil. A critical evaluation of his work by Shipman (2001) shows that his scientific work was innovative and erudite, contrary to reports circulated by paleoanthropologists and science historians. The contemporary reviews of his 1895 monograph by, e.g., the German anatomist Wilhelm Krause and the multitalented scientist Rudolf Virchow were scathing, just as were those of British, French, and Swiss scientists. On the other hand, it was no surprise that Haeckel's comment was positive. The skepticism of part of the scientific community incited him to tremendous activity, and there resulted a flow of papers on *Pithecanthropus*. It is thanks to Dubois that the focus on human fossils increased (Shipman and Storm 2002). The marketplace for human fossils and paleoanthropological discussions was open (Sander 1976).

Among the scientific activities at the turn of the penultimate century of anthropological organizations in different European countries, e.g., the Gesellschaft für Anthropologie, Ethnologie und Urgeschichte in Berlin or the Société d'Anthropologie de Paris as well as the Royal Anthropological Society of Great Britain, interest in the diversity of recent humankind was paramount. While many activities were concentrated on the typological classification of recent populations as well as prehistorical and archaeological research, paleoanthropological problems and fossils played only a minor role. Dennell (2001, p. 52) designates the period from ca. 1870 to 1930 as the "Age of Prejudice so far as European (and North American) perceptions of non-whites is concerned." The dominating theme was the racial prejudice of fixity and inequality of races. While this attitude did not change when the first non-European fossil caught the interest of scientists and the public in general, it introduced a new aspect of human evolution: the confrontation of Eurocentric typological views with paleoanthropological facts (Hoßfeld 2005a, b; Henke 2010a, b; Henke and Hardt 2011; Henke and Herrgen 2012).

In the light of the *Pithecanthropus* fossils, the Neanderthal problem reached a new dimension. Virchow's diagnosis implied that the Neanderthal man was diseased with rickets as a child and arthritis as an adult. To many, this explanation of the special bony features of Neanderthals sounded farfetched (Trinkaus and Shipman 1993). There was a fundamental need for appropriate comparative biological research and a reasonable taxonomic approach. With the benefit of the hindsight, one can see that in those times there was no theoretical basis for paleoanthropological research, since the anatomists as well as the archaeologists were concentrating on case studies, while zoologists, like Haeckel (1866), were focusing on other topics than merely paleoanthropology. The end of the nineteenth and the beginning of twentieth century yielded exciting discoveries of human fossils (Table 1). The obvious lack of a sophisticated theoretical basis and elaborate methodological skills in paleoanthropological research gradually led to the development of a new field of evolutionary biology.

Table 1 Timetable of the unearthing and interpretation of human fossil remains and relevant breakpoints of paleoanthropological research before 1930

Year	Place and site	Specimens, taxon, pathbreaking finding	Aspects and comments
1830	Engis, Belgium	First Neanderthal fossil, Mousterian culture	Described much later as such
1848	Forbes' Quarry, Gibraltar	Neanderthal calvarium	Described much later as such
1856	Kleine Feldhofer Grotte (Neanderthal, Germany)	Calotte and postcranial skeleton, no archaeological remains	First human fossil remains which have been attributed by Fuhlrott and Schaaffhausen in 1857 as diluvial remains, detailed description by Fuhlrott in 1859
1859	London (UK)	Charles Darwin publishes his "Origin of Species by Means of Natural Selection . . ."	Darwin's descent theory and his explanatory theory of selection induced a paradigmatic change
1866	La Naulette (Belgium)	Mandible, Würm I	Further indication for the existence of fossil man
1868	Cro-Magnon (France)	Fossil remains of several individuals, best known as "Le Villard" (Cro-Magnon 1), type specimen of a so-called Cro-Magnon race within contemporary typological classifications of those times	The fossils have been described by Vacher de Lapouge as *H. spelaeus* but are fully modern Upper Paleolithic humans. The association of the "Cro-Magnon" type with an (evolved) Aurignacian and an extinct Pleistocene fauna was essential for the acceptance of a human antiquity
1880	Šipka (Czech Republic)	Fragmentary mandible of a child, Mousterian, Würm I/II	The Neanderthal mandible did not convince the critics of the evolutionary theory
1886	Spy (near Namur, Belgium)	Two skulls and postcranial remains	The morphology of the bones disproved any doubt on the existence of Neanderthal man in Europe
1887–1892	Taubach (Germany)	Isolated teeth, Mousterian culture	"Pre"-Neanderthal remains
1891–1898	Trinil (Central Java, Indonesia)	Calotte and complete femur, partial femur, teeth	The discovery of the Trinil fossils by Eugène Dubois (*Pithecanthropus erectus*) was essential for the discussion of the "missing link" and displaced the focus on human origins from Europe to Asia

(*continued*)

Table 1 (continued)

Year	Place and site	Specimens, taxon, pathbreaking finding	Aspects and comments
1899–1905	Krapina (Croatia)	>670 cranial remains, Riss-Würm Interglacial, cannibalism, burnt bones, Mousterian culture	The "*H. primigenius*" (later on *H. neanderthalensis*) was excellently described and analyzed by Gorjanović-Kramberger (1906)
1907	Mauer (near Heidelberg, Germany)	Fossil mandible, dated to the middle Pleistocene, between the Cromerian and Holsteinian interglacials, ca. 500 ka	Schoetensack (1908) described the Mauer jaw as a new species, *H. heidelbergensis*. Some regard the fossil as *H. erectus* or classify the specimen as archaic *H. sapiens*
1908	La Chapelle-aux-Saints (France)	Well-preserved Neanderthal skeleton with a lot of pathologies, Charentian, Mousterian, Würm II	Boule's description of the fossil (1911–1913) was a milestone of research of the Neanderthals and "established" them as a separate species of their own; long time regarded as "archetype" of the classic Neanderthals of western Europe
1908	La Quina (France)	Remains of a total of 27 hominin individuals, highly fragmentary, including an infant skull (H 18); Quina variant of the Mousterian, traces of fire	Louis Henry-Martin described the fossil material in 1908 and in the following years as classic Würm Neanderthal remains
1908/1914	Le Moustier (France)	Adolescent and infantile skeleton, associated with Mousterian culture and overlying Châtelperronian assemblage	Described by Klaatsch and Hauser (1910) as the type specimen of the species *H. mousteriensis*, although the Neanderthal affinity of the specimens has never been disputed
1908–1915	Piltdown (Sussex, England)	From "Pleistocene gravels" "unearthed" specimen, a chimera of an intentionally manipulated mandible of a juvenile orangutan and portions of the skull of an anatomically modern man	The specimen was named *Eoanthropus dawsoni* and caused a lot of trouble in paleoanthropology as most of the leading British paleoanthropologists regarded the fossils authentic

(*continued*)

Table 1 (continued)

Year	Place and site	Specimens, taxon, pathbreaking finding	Aspects and comments
1908–1913 and 1914/ 1916/1925	Weimar-Ehringsdorf (Germany)	Calvaria, parietal, mandible, teeth, older than the classical Neanderthal man, Mousterian culture	“Pre”-Neanderthal remains
1909–1912 1920–1921	La Ferrassie (France)	Fossil material of two adult and several highly incomplete and poorly preserved immature individuals, crouched burials	Field descriptions by Capitan and Peyrony (1909, 1911–1912) and detailed analysis by Boule (1911–1913)
1918 f.	Zhoukoudian (near Beijing, China)	Zdansky collected in the large karst cave human teeth and Bohlin started the excavation campaign 1928–1929 followed by further excavations	The successful excavation of the site shifted the focus of paleoanthropological research and the origin of mankind entirely to Asia. Black’s description of *Sinanthropus pekinensis* established a species very similar to *P. erectus*
1921	Broken Hill (newly Kabwe; near Lusaka) Zambia (formerly Rhodesia)	The well-preserved calvarium is associated with an African MSA, dated to 200–125 ka	Woodward (1921) classified the “Rhodesian Man” as a new species *H. rhodesiensis* and Pycraft (1928) opted for a new genus *Cyphanthropus rhodesiensis*, while Mourant (1928) saw Neanderthal affinities. Actually the specimen is mostly attributed to *H. heidelbergensis*
1924	Taung (North West Province, South Africa)	The skull and hemiendocast of a child have been described by Raymond Dart (1925) in a *Nature* article as species nova *Australopithecus africanus*	The characters in Dart’s *A. africanus* were diametrically opposed to those expected; for this reason his classification was highly criticized by Woodward and Keith, the contemporary leading British paleoanthropologists
1924–1926	Kiik-Koba (Crimea, Ukraine)	Hominid remains including an adult male and an infant (possible burials) assigned to *H. neanderthalensis*, Mousterian occupation level, Würm I	Extension of the distribution map of Neanderthal sites to eastern Europe

(*continued*)

Table 1 (continued)

Year	Place and site	Specimens, taxon, pathbreaking finding	Aspects and comments
1926	Gánovce, Slovakia	Cranial and postcranial remains, Riss-Würm Interglacial, Mousterian culture	“Pre-Neanderthal” remains
1927	Mugharet el-Zuttiyeh, near Lake Galilee, Levante (today Israel)	Frontal skull fragment with an intermediate morphology, neither modern nor Neanderthal	First human fossil remain from the crossroads of the Middle East Corridor
1929	Saccopastore near Roma (Italy)	Clavarium (Saccopastore 1), skull fragments, upper jaw, Riss-Würm Interglacial	“Pre”-Neanderthal remains from stage 5e (130–120 ka)

Compiled from Henke and Rothe (1994, 1999a, references given there)

The best basis for such a development existed in France, where Pierre Marcelin Boule (1861–1942), a qualified geologist, paleontologist, and archaeologist, unified all necessary attributes to establish a program for paleoanthropology. His classical description of the Neanderthal skeletons from La Chapelle-aux-Saints (Boule 1911–1913) was a landmark in the history of human paleontology (Heberer 1955a). Contemporaneously, the German anatomist Gustav Schwalbe (1844–1916) analyzed a skull fragment from Eguisheim as well as the famous Javanese *Pithecanthropus erectus* (Schwalbe 1906; Fischer 1917): research that is regarded as critical to the founding of paleoanthropology as a research field of its own. Heberer (1955b, p. 298) comments on this: “An die Stelle ungenügend fundierten Theoretisierens tritt jetzt in der menschlichen Fossilforschung die exakte Empirie.” Albeit this sounds somewhat effusive, the empirical approach to the morphological and metrical analysis of the fossils allowed an independent development separate from geology and archaeology. This view characterizes, on the one hand, the poor cooperation of paleoanthropology, as a biological field of research, with the geosciences as well as with archaeology/prehistory and, on the other hand, the overestimation of the scientific importance of quantifying morphological methods (Chaoui 2004; Hoßfeld 2005b). Both of these aspects hampered any essential progress in paleoanthropology for decades, the subject remaining mainly narrative and descriptive (see Hoßfeld 2005a, b; Henke 2006a, b, 2010a, b; Blanchard 2010).

Development of Principles and Methodical Skills in Paleoanthropology

Neither Haeckel nor Virchow regarded paleoanthropology as a particularly important subject, and even anthropology itself was not a discipline of great significance in their times. The reason for the late establishment of anthropology as a separate

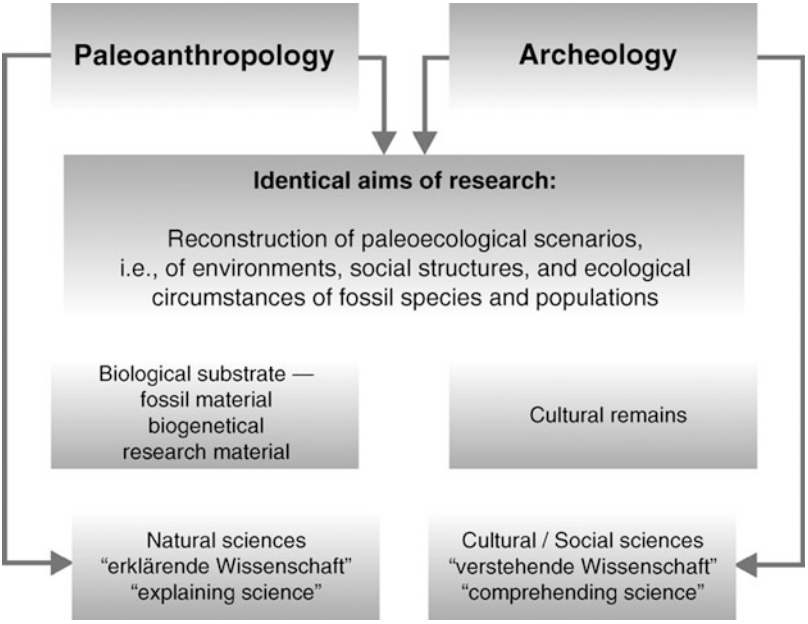


Fig. 5 Paleoanthropology versus archaeology – identical aims but different approaches (Henke and Rothe 2006)

biological discipline is, as Grimm (1961, p. 1) suggested, that "der Anthropologe viel weniger als der Zoologe oder der Prähistoriker oder der Anatom in der Lage schien, die Grenzen seines Faches zu bestimmen."

In the first half of the twentieth century, paleoanthropology remained uncentered as physicians, anatomists, biologists, archaeologists, and ethnographers from different viewpoints and with different intentions and aims all practiced anthropology (Henke 2010a, b). This becomes especially obvious if one looks from the more zoological fields of research across to archaeology. The division of so-called explanatory natural sciences (erklärende Naturwissenschaften) from the comprehending humanities (verstehende Geisteswissenschaften) sensu Dilthey 1883 (Groethuysen 1990) was completed at the beginning of the twentieth century, contingent on the obvious consciousness of superiority of natural sciences (Fig. 5).

The rediscovery of Gregor Mendel's laws in 1900 by Carl Correns, Erich von Tschermak-Seysenegg, and Hugo de Vries gave a push to evolutionary thinking. Around 1930, protagonists of neo-Darwinism like Ronald A. Fisher, John B. S. Haldane, and Sewall Wright developed the basic principles of population genetics and induced a fruitful diversification of natural sciences. In the following period, the Russian-American geneticist and evolutionary biologist Theodosius Dobzhansky (1900–1975), the American paleontologist George Gaylord Simpson (1902–1984), the German evolutionary taxonomist Ernst Mayr (1904–2005), and finally the British biologist Julian Huxley (1887–1975) founded the Synthetic Theory of

Evolution, integrating additionally quite a number of neighboring disciplines to reconstruct the phylogenetic process of our own origin (Jahn et al. 1982; Jahn 2000; Junker 2004; Wuketits and Ayala 2005; Hoßfeld 2005a, b). The major principles of the "Synthesis" itself were subsequently enunciated between 1937 and 1944 in three seminal books. While Dobzhansky (1937) focused on the gene, Mayr's (1942) vantage point was the species and Simpson's (1944) perspective was on the higher taxa. Tattersall's (2000a, p. 2) assertion that "the Synthesis was doomed to harden, much like a religion," is controversial (see, e.g., Foley 2001). However, before we discuss the consequences of the "Synthesis" (for alternative terms, see Junker 2004), we shall have a closer look at paleoanthropology.

Fossils: Hypotheses, Controversies, and Approaches

In the early days of paleoanthropology, the main question was quite simple: Is there a fossil record that proves the existence of our ancestors from ancient times? The protagonists of paleoanthropology soon recognized the need for a more sophisticated empirical approach. The best basis for such a development existed in France, where Pierre Marcelin Boule, just mentioned, unified *in persona* all necessary attributes to establish a qualified paleoanthropology. His classic study of the Neanderthal skeleton from La Chapelle-aux-Saints (Boule 1911–1913) became a landmark in the history of human paleontology (Heberer 1955a). He aimed to understand the patterns of variation and the significance of anatomical differences. For this reason, Boule invented special instruments for quantification and simple statistical concepts to analyze the variation in human skeletons (Boule 1921, 1923; Boule and Vallois 1946, 1952). Boule established a paleontology of humans, later on called paleoanthropology, as a scientific discipline; but as evolution itself was still regarded as a widely speculative myth, the debate on human evolution "rose and fell like a tide in France, Germany, England, and the United States," as Trinkaus and Shipman (1993, p. 154) described the situation.

During the late nineteenth and the early twentieth centuries, an overemphasis quantifying procedures strongly affected the anthropological research, starting with the first occupants of anthropological chairs, Jean Louis Armand de Quatrefages de Breau (1855, Paris) and Marcelin Boule (1867, Paris), as well as Johannes Ranke (1886, Munich) and Felix v. Luschan (1900, Berlin). While Ranke was deeply opposed to the idea of human evolution, with Otto Schwalbe, just mentioned, Theodor Mollison (München), Felix v. Luschan (Berlin), Rudolf Martin (München), and Otto Schlaginhaufen (Zürich) successively advocated measuring techniques of every conceivable kind (Keller 1995; Chaoui 2004; Junker 2004; Hoßfeld 2005b). While Schwalbe was convinced that information on evolutionary history could only be gained from neo- and paleozoology, others focused predominantly on typological classification of prehistorical populations and neglected broader paleoanthropological questions. This can only be understood by the fact that the conventional wisdom of that time was that modern "races" arose from types that were already separate in the early Pleistocene. For this reason, there was a big problem when Gorjanović-Kramberger (1906) described the fossils from Krapina, excavated in 1899–1905, in a voluminous monograph as belonging to a "man-eating" population (Radovčić et al. 1988). As this thesis was accepted by one of the most outstanding anthropologists of the time, Aleč Hřdlicka (Prague, later on Washington), who pushed paleoanthropological research using his influential position at the Smithsonian Institution, Krapina became a big challenge to the scientific community (Henke 2006a). Notwithstanding the problem that the assumed anthropophagy/cannibalism of the Neanderthals remained controversial (see, e.g., Ullrich 1978, 1995, 2005a; Orschiedt 2008), it must be emphasized that Gorjanović-Kramberger (1856–1936) did excellent geological, paleontological, paleoanthropological, and archaeological research far ahead of the standards of his time (Frayer 2006; Henke 2006a). Tim White (2006, preface) lauded him in the centennial bibliography, edited by Frayer, thus: "His osteological and archaeological skills brought the valuable Krapina remains and their contexts to light. His paleoanthropological insights are embedded in a body of scholarly writings (1899–1929) foundational to modern paleoanthropology." And Frayer (2006, p. 3) refers to the publications of Jakov Radovčić (1988) and Radovčić et al. (1988):

"Gorjanović-Kramberger was first

1. to preserve and map a detailed stratigraphic profile of a Neandertal site,
2. to save virtually every Neandertal fossil he encountered from the four tooth germs to the 16, mostly complete patellas,
3. to number the fossils and record the levels from where they derived,
4. to save most of the faunal remains and all the stone tools,
5. to use the emerging field of radiology for documenting Neandertal morphology,
6. to conduct trace element analysis as a relative dating technique for confirming the contemporaneity of fossil mammals and humans,
7. to publish multiple, quality photographs of the hominin fossils and
8. to propose and document cannibalism in the fossil record based on burned specimens, cut marks and other bone damage."

What might he have done further? I confess that Gorjanović-Kramberger is my favorite as most innovative paleoanthropologist of his time (see Henke 2006a), followed by Gustav Schwalbe, anatomist at the University of Strasbourg, whose comparative morphologic research on fossils (e.g., *Pithecanthropus* from Java, Neanderthal calotte, Eguisheim, Brüx, *Oreopithecus*) was setting standards.

Compared to the two protagonists just mentioned above, the image of Hermann Klaatsch (1863–1916; Breslau) is colorful and iridescent; his research output varies from highly elaborated to suspect. The excavator (together with Otto Hauser [see, e.g., Drößler 1988; Drößler et al. 2006]) and researcher of the fossils from Le Moustier and Combe-Capelle was, e.g., wrong about the "sleeping position" of Le Moustier 1 (see Ullrich 2005a, b; Hoffmann 2003a, b), and his papers on Combe-Capelle are – to say the least – under suspicion, since it became known by the radiocarbon calibration of the newly recovered skull that the icon of the

Aurignacian, the earliest period of the Upper Paleolithic, is not older than late Mesolithic (Hoffmann et al. 2011; Henke 2011). These results are both irritating and suspicious, as Klaatsch "used the fossil record to support his polygenist view, and one way he could do so was to show that the Neandertals and Aurignacians (races he believed had separate origins) coexisted" (Wolpoff and Caspari 1997, p. 127; for more details, see Henke 2011).

Further controversies were born when descriptions of the Upper Paleolithic skeletons from, e.g., Chancelade, Grimaldi, Combe-Capelle, and Oberkassel, and also Neanderthals such as Le Moustier, La Chapelle-aux-Saints, La Ferrassie, and La Quina were excavated and published (Henke et al. 2006). There was special interest in the mandible from Mauer that was described in 1908 by Otto Schoettensack (1850–1912) as *Homo heidelbergensis* (Adam 1997; Wagner and Beinhauer 1997; Hardt and Henke 2007; Wagner et al. 2007; Henke and Hardt 2011).

In England, the motherland of Darwinism, there was for a long time little progress in paleoanthropology since the alleged Darwinists were obviously "no Darwinians in the modern sense" (Bowler 2001, p. 14). During the period from 1860 to 1940, a Darwinian style of explanation began to replace non-Darwinian developmental models stepwise, but a real breakthrough or turnover did not occur before World War II, largely due to the overwhelming influence of the paleontologist and geologist Arthur Smith Woodward (1864–1944) and the zoologist Sir Arthur Keith (1866–1955) as the leading authorities on human remains. Keith published *An Introduction to the Study of Anthropoid Apes* in 1896 (see also Keith 1911), followed by a monograph, *The Antiquity of Man*, which appeared in 1915. This publication on all-important fossil human remains founded his worldwide reputation and appeared in an enlarged edition in 1925. As can be seen from his textbook *Concerning Man's Origin* (Keith 1927), he was at that time less convinced than he had been 10 years before that modern humans and extinct "primitive" types had lived contemporaneously. In his volume *New Discoveries*, Keith (1931) rejected this interpretation given the strength of the arguments for an evolutionary branching of hominins. From the viewpoint of history of science, we have to ask why the leading "anthropologist" as well as his compatriot Sir Grafton Elliot-Smith (1871–1937) retained this view for so long in the face of compelling contrary arguments from paleoanthropological discoveries in Europe, Asia, and after 1925 in South Africa too.

One plausible explanation is that theories are the filters through which facts are interpreted as Popper (1959b) said. The reason why the English authorities adhered to wrong models combines the fatal misinterpretation of the Piltdown hoax with wishful thinking and cultural bias (Spencer 1990a).

The background of the Piltdown forgery has been analyzed and described many times (Spencer 1990a, b). The most plausible explanation why the *Eoanthropus dawsoni* hoax was so successful is that it seemed to provide proof for a missing link between apes and humans, using a mix of plesio- and apomorphic characters. Especially, the primitive jaw and dentition made *Eoanthropus* a more suitable intermediate candidate than *Pithecanthropus*. Even after the discovery of *Australopithecus* at Taung in 1924, and the excavation of the first *Sinanthropus* skull from

Zhoukoudian (Chou-kou-tien) shortly thereafter, Keith (1931) hypothesized that the Piltdown type arose from the main ancestral stem of modern humanity.

At that time, prominent British anthropologists such as Smith Woodward, Keith, and Elliot Smith were fixed on a European origin of humankind and absolutely in opposition to models of Asian and African origin. The expected phylogenetic sequence was that the cerebralization antedated the changes of the viscerocranium. As the plesiomorphic jaw and the apomorph brain of *Eoanthropus* complied with this expectation, it fitted perfectly into a scheme that was in fact wrong. One could comment on this "credibility of the plausible" in Plato's (The Republic, 382d) word: "And also in the fables of which we were just now speaking, owing to our ignorance of the truth about antiquity, we liken the false to the true as far as we may" (see Stoczkowski 2002, p. 168).

It took more than 40 years before Joseph S. Weiner (1915–1982), Sir Kenneth P. Oakley (1911–1985), and Sir Wilfrid Le Gros Clark (1895–1971) jointly exposed the hoax, although there was much skepticism and rumor earlier. Whoever the players were in this black mark in science, they were aware of the attractiveness and fascination of fossils, the rare resources that help to decipher our place in nature, and they obviously knew about the public appeal (Stringer and Gamble 1993; Walsh 1996; Weiner and Stringer 2003; overview in Harter (1996–1997) www; Turritin (1996–1997) www). The interpretation of the Piltdown fossil as a human precursor was partially responsible for the vehement dismissal of the first *Australopithecus* from South Africa. Dart's interpretation of the Taung child as missing link between ape and man yielded a storm of controversy (Tobias 1984). As Trinkaus and Shipman (1993, p. 206) put it: "The entire scientific coterie of Britain believed in the fossils without hesitation." This is remarkable insofar as Dart's discovery matched the prophecy of Darwin (1871, p. 202): "It is, therefore, probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee: and, as these two species are now man's nearest allies, it is somewhat more probable that our progenitors lived on the African continent than elsewhere."

To the extent that these and other indications for an extra-European "cradle of humankind" were deliberately ignored, the Piltdown case is a telling example of cut and dried opinions. Are there more self-fulfilling prophecies? It may be that Klaatsch's "contradictions and fanciful reconstructions" (see Zängl-Kumpf 1997, p. 575), and especially his polygenist view, influenced his interpretation of the Le Moustier and Combe-Capelle fossils (Henke 2011). If paleoanthropologists see what they please, small wonder that the scientific output of paleoanthropology during the first decades of the last century was very heterogeneous and confusing and more redolent of stagnation than progress. The evolutionary biology at those times was characterized by Mayr as "chaotic" (Tattersall 2000a, p. 2). But why?

First, even at the beginning of the twentieth century, Darwin's principles were widely misunderstood by anthropologists, who persisted in orthogenetic biological thinking or insisted on the theoretical split between natural sciences and humanities. Paleoanthropological theory and methodology were still in statu nascendi, judging from the literature of the time (Klaatsch 1899; Hrdlička 1914; Werth 1921; Weinert 1928; Wiegers 1928; Abel 1931; Hooton 1931; Keith 1931; Le Gros Clark 1934).

Second, the rediscovery of Mendel's work in 1900 demonstrated that new hereditary variation, i.e., mutation, occurs in every generation and every trait of an organism. The founding of genetics at the beginning of the twentieth century gave tremendous support to Darwin's theory and removed the objections to his postulates. However, the effects of genetics and population genetics were felt less in paleoanthropology than in the biology of recent populations and especially in aberrations like typological social biology, ethnogeny, and race typology. In Germany, social Darwinism and fatal concepts of hereditary and race dominated biological and medical research on living people. Paleoanthropology was of only minor interest, while the aim of anthropology was defined in the national socialist area or "the Third Reich," ". . . der deutschen Volksgemeinschaft zu dienen" (Reche 1937; see further Zmarzlik 1969; Gould 1983; Müller-Hill 1988; Seidler and Rett 1988; Weingart et al. 1988; Zängl-Kumpf 1992; Hoßfeld and Junker 2003; Junker 2004; Hoßfeld 2005a, b; Preuß 2009).

Third, various approaches to explain the process of hominization later on turned out to be politically highly incorrect: e.g., Kollmann created in 1885 the term "neoteny" suggesting that humans evolved from pygmies who had simply retained juvenile features during size increase (Kollmann 1902). The basic idea was that pygmy progenitors probably arose from juvenile apes that had lost the ancestral tendency to regress. Bolk (1926) argued in a long series of papers that man evolved by retaining the juvenile features of his ancestors. His "fetalization hypothesis" influenced evolutionary thinking on human origins and formed expectations of the appearance of transitional species. Bolk's theory was highly criticized and later on rejected by Starck (1962) because it was built on flawed arguments and a misinterpretation of Darwin's principles. Similar questions still resound in the current so-called evo-devo discussion, e.g., the evidence overwhelmingly suggests that neoteny, the retention of juvenile characteristics, was one of the most important processes involved in the origin of *H. sapiens* (Minugh-Purvis and McNamara 2002).

Fourth, the discovery of numerous Neanderthal skeletons (Table 1) caused new arguments in the discussion of gradualism versus continuity. Boule's monograph evicted the Neanderthals from our family tree, although some outstanding early twentieth-century paleoanthropologists like Aleč Hrdlička argued for gradualism, a controversy that continues to this day (overview in Wood and Lonergan 2008; Cartmill and Smith 2009; Henke and Hardt 2011; see also below).

Finally, the non-European fossils from, e.g., Java, China, and South Africa, could have been a strong stimulus for a wider view of human origins (for details on the history of contemporary excavations, see, e.g., fossil catalogues by Schwartz and Tattersall 2002, 2003, 2005; encyclopedia by Delson et al. 2000; and textbooks by Cartmill and Smith 2011). However, the prejudice of the leading British scientists crushed innovative hypotheses, and the critical skepticism on non-European roots of humankind due to Eurocentric perspectives and the fatal misinterpretation of the Piltdown man resulted in a stagnation of paleoanthropological theories. Dennell (2001, p. 51) puts it this way: ". . . it is depressing to realize how much of what was written on human origins before WWII was little more than prejudice masquerading as science, it is impossible to understand the study of human origins without reference to these prejudices" (see also Stoczkowski 2002; Hoßfeld 2005b; Junker 2004; Delisle 2007; Henke 2010a, 2011).

Paleoanthropology, Ideology, and Politics: Symptomatic Events

The misapplication of the Darwinian biological theory known as social Darwinism has been intensively discussed in another context (Mühlmann 1968; Zmarzlik 1969; Altner 1981a, b; Müller-Hill 1988; Weingart 1988; Hofstadter 1995; Hawkins 1997; Dickens 2000; Junker 2004; Hoßfeld 2005b). It is well known that this biological ideology was the "Janus head" of scientific Darwinism (Altner 1981b) from the beginning; however, it became highly influential and threatening after World War I, especially during the period of National Socialism in Germany. That paleoanthropology was no free zone of research stems from different reasons: first, because paleoanthropology was a subdiscipline of the highly politically involved physical anthropology (Weingart et al. 1988; Hoßfeld 2005a, b) and second, because racial thinking and racist theory were interwoven with all aspects of daily life (Bowler 1976; Stepan 1982; Bowler 1986, 1988, 1996, 1997, 2001; Proctor 1988; Weingart et al. 1988; Vogel 1983, 2000; Hoßfeld 2005a; Preuß 2009; Henke 2010b; 2011) – long before the fascistic "Third Reich" in Germany began. The following symptomatic cases are discussed to exemplify pars pro toto and exemplarily the impact of social Darwinism, ethnocentrism, and racism on paleoanthropology.

First Case: Hermann Klaatsch's Iridescent Image

As mentioned above, Hermann Klaatsch, a German comparative anatomist, anthropologist, prehistorian, and ethnologist who headed the Institute of Anthropology and Ethnology in Breslau (today Wrocław) since 1907 till his sudden death in 1916, was one of the most prominent paleoanthropologists in his time. He started an excellent career under the renowned anatomist Karl Gegenbaur (1826–1903; Heidelberg). The young researcher was impressively noticed by the scientific community of physical anthropologists at the Anthropology Congress 1899 at Lindau, where he presented a paper "About man's place among the mammals, especially the primates and the mode of evolution from an earlier form" (Klaatsch 1899, 1900). Advocating for the application of Darwinian principles to humans, Klaatsch received fierce criticisms from the doyens Virchow and Ranke (see Trinkaus and Shipman 1993; Wolpoff and Caspari 1997; Hoßfeld 2005a, b; Weniger and Klaatsch 2005; Henke 2006a, 2011). Evans (2010, p. 81) states that Klaatsch was the only physical anthropologist in German-speaking anthropological circles besides Gustav Schwalbe (and Hermann Schaaffhausen who died 1893) who championed Darwinism at the late 1890s. I would like to add Dragutin (Karl) Gorjanović-Kramberger who was trained in Germany and maintained close contacts to Schwalbe (see Henke 2006a) but was on slippery ground with his colleague from Breslau, after having refused joint research on the Krapina fossils. Trinkaus and Shipman (1993, p. 168) describe Klaatsch's motives for a cooperation as follows: "the fossils were someone's ticket into the brightly lit heart of anthropology, and Klaatsch lusted after them."

Klaatsch had done doubtless excellent innovative comparative research on primates and human fossils, e.g., the Neanderthal calotte (citations see Wegner and Klaatsch 2005); but, he didn't have priority access to human fossils. It has been suggested that this deficit gave the impetus for his Australian expedition from 1903 to 1907; however, there may have been other reasons, including the "*Out-of-Australia*" theory of his close friend Otto Schoetensack (1850–1912) who developed the notion that the human race in fact originated in Australia (Schoetensack 1901, 1904). In this he was influenced by Thomas H. Huxley who had visited Australia earlier, looking for the origin of mankind in the fifth continent. Corinna Erckenbrecht (2010, p. 49) suggests in her biographical-ethnological thesis on Hermann Klaatsch: "As Schoetensack himself was in poor health it was agreed upon that Klaatsch was to make the trip to Australia."

Her conclusions on the "Personality of Klaatsch as a Scientist and His Ethics of Collecting" are complex; on the one hand, she describes Klaatsch as "a very versatile, well educated and trained scientist who thought in major scientific and theoretical contexts on a high level." On the other hand, she reveals: "To enforce his personal research interests he acted in a very energetic, sometimes uncompromising way without respect for the feelings and values of the Aborigines." In contradiction to this attitude, "he publicly stood up for the rights of the indigenous people, criticized their treatment by the white Australian society" (Erckenbrecht 2010, p. 49). Though one may explain his conflicting behavior as compromisingly assertive, on the one hand, and paternalistically protective, on the other hand, as an attitude of social Darwinistic superior-inferior thinking, and typical of a colonialist mentality, it is in modern terms of political correctness simply unethical.

For historiographical reasons, we must ask how this personality may have influenced Klaatsch's paleoanthroplogical research. In 1907 Klaatsch returned to Germany and cooperated highly successfully with the Swiss art dealer and archaeologist Otto Hauser (1874–1932; Drößler 1988; Hoffmann 2003a, b; Drößler et al. 2006), excavating and analyzing the famous skeletons of Le Moustier and Combe-Capelle (Hoffmann 2003a, b; Ullrich 2005a). The French historian Benoit Massin (1996, p. 88) describes that Klaatsch, "previously an advocate of the unity of mankind," made a dramatic about-face at the 1910 meeting. On the basis of comparative morphological study of prehistoric human races, Klaatsch argued that there were two main branches of human evolution: one Western stock from which emerged the gorilla and Neanderthal man and one Eastern stock for the orangutan and the Aurignacian race (Klaatsch 1910a, see pp. 91ff; see further Klaatsch 1911; Henke 2011).

Evans (2010, p. 65) adds: "Klaatsch's polygenist ideas won few adherents, however, and the resistance that he engendered, confirmed the monogenist consensus." From the beginning, Combe-Capelle's high early Aurignacian age was

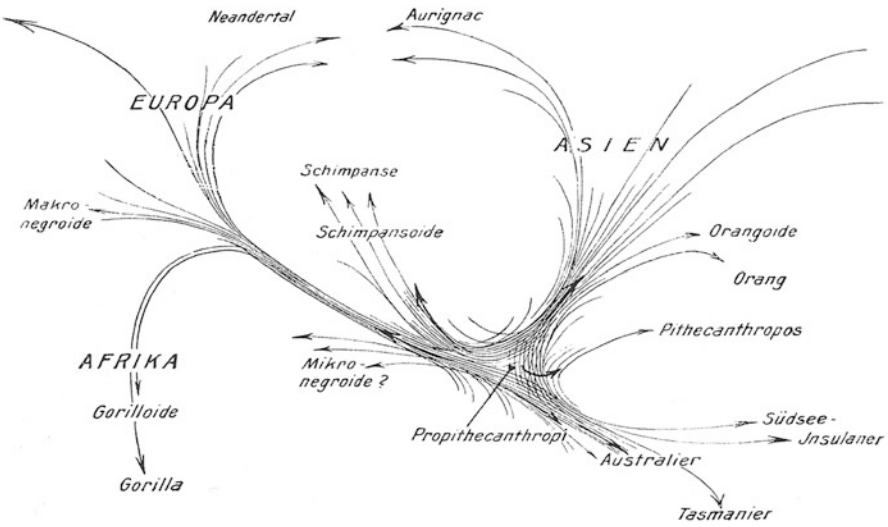


Fig. 6 Klaatsch's polygenist tree, assuming different roots of the Neanderthals and the Aurignac Man (Klaatsch 1911, p. 480)

heavily criticized, though it fitted perfectly in Klaatsch's phylogenetic scheme (Fig. 6). As it recently turned out after the surprising rediscovery of the individual and radiocarbon dating that showed merely an early Holocene age (Hoffmann et al. 2011), there arose many unpleasant questions, e.g., the suspicion that Klaatsch and Hauser might have preferred the greater age for unscientific reasons. Though this isn't proof, there remains a bad aftertaste; however, *in dubio pro reo*! As has been demonstrated by a historical analysis of the literature on Combe-Capelle (Henke 2011), the false calibration of the Upper Paleolithic icon Combe-Capelle had tremendously influenced paleoanthropological theories during the first half of the last century. This is not trivial, insofar as the "Aurignac Man" played a prominent role in the contemporary racial typologies, e.g., the Nordicism, an ideology of racial supremacy and "master race" racism (e.g., Weinert 1941). Apart from this, one might mention that both authors profited – Klaatsch earned scientific praise and Hauser additionally thousands of Reichsmarks because Combe-Capelle was thought to be the oldest anatomically modern human fossil worldwide: *Honi soit qui mal y pense*! Though historians will quite likely not be able to solve the problem of whether the diagnosis was a deliberate move on the part of Klaatsch, or was simply a self-fulfilling prophecy, this case should be a lesson "to see what we are looking at, not to put it in a preferred scheme" (sensu W.W. Howells 1993). Furthermore, this case should make us cautious, as not every scientist knows the guidelines of good and ethical practice (see Wuketits 2010, 2012), and sociobiologists would comment laconically: Never suppose a positive cause, if there could be a negative one.

Second Case: Political Constraints, See What "We" Want

That archaeological and paleoanthropological researches were not spared by the ideology of the national socialists is documented, e.g., by the fact that the Neanderthal Museum, which had been inaugurated on May 1, 1937, was closed by order of the Reichsleiter für Vorgeschichte, Reinertz, on March 3, 1938. The arguments were that the museum, which should demonstrate "Deutsche Urgeschichte, soweit sie mit dem Neandertal in engster Beziehung steht," did not pass the evaluation of an NS commission (Beckmann 1987).

This case may be a warning that (paleo)anthropological exhibitions in museums and all kinds of popular scientific media are interpretatively filtered through ideologies and personal perceptions of the curators and authors (see, e.g., Ickerodt 2005; Sarasin and Sommer 2010). Additionally, one must be aware that this equally applies to all kinds of science and knowledge transfer (Henke 2007a, 2010a).

Third Case: Franz Weidenreich, Politically Unwanted

Even more inimical to the development of paleoanthropology during the Nazi era was the fact that the most outstanding German paleoanthropologist at that time, Franz Weidenreich (1873–1948), lost with effect from December 31, 1935, his *venia legendi* at the Johann Wolfgang Goethe University due to the persecution of the Jewish population (Hertler 2007). His emigration to the USA was an irreplaceable loss for anthropology in Germany.

Exempla docent – after Hubert Markl, former president of the Max Planck Society, we should learn from good *and* bad experiences in our history; in the latter context, history of science plays a most significant role. The well-known biography of most famous scientists, e.g., Albert Einstein, Ernst Mayr, and Erwin Chargaff, is impressive proof that "science serves with heads." Markl's (1988) identical worded article "Wissenschaft dient mit Köpfen" convincingly shows that the scientific community needs internationality: "Wir wissen auch, daß manche dieser Netze buchstäblich zum lebensrettenden Sprungtuch auf der Flucht vor Verfolgung geworden sind und immer wieder werden. Niemand hat diese Weltbürgerschaft des Wissenschaftlers überzeugender deutlich gemacht als Albert Einstein" (Markl 1988, p. 116–119).

Since Franz Weidenreich was involved in research on the largest *H. erectus* sample from a single locality, Zhoukoudian, paleoanthropology in Germany lost a vital contact with the international scientific community. Thanks to Weidenreich (1943), brilliant documentation, casts, and descriptions survived of the "*Sinanthropus*" – skulls which were lost during an attempt to ship them to the USA (Shapiro 1974) – and, equally important, Weidenreich is viewed as the founder of the "multiregional theory of human evolution" (Wolpoff and Caspari 1997; Wolpoff 1999; Hertler 2007; for a popular scientific biography, see Hartkopf 2012). Weidenreich's illustration (see Fig. 7) of the process of human evolution became known as "trellis," a network of populations by gene exchanges. Wolpoff and Caspari (1997, p. 200) explicate the graphic as follows:

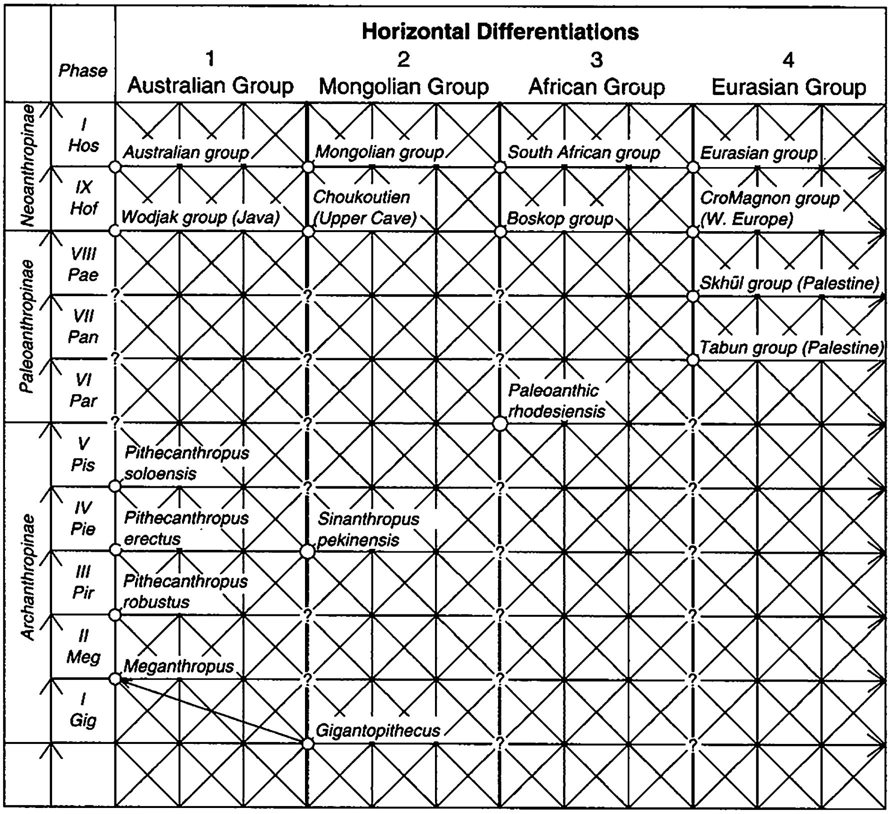


Fig. 7 Pedigree of the Hominidae, so-called trellis, from Weidenreich (1946, p. 30) (Redrawn by Wolpoff and Caspari 1997, p. 201)

"[trellis], a network with vertical lines passing through the main stages of evolution, horizontally separated into the main centers of evolution (distribution and specialization), and the diagonal connections between them reflecting the patterns of genetic exchanges," in Weidenreich's own explanation, "a graphic presentation of the conception of the hominid group as one species" (Weidenreich 1946, p. 30).

This "trellis" or "lattice" expresses Weidenreich's idea that evolution is transformation, in close connection with interbreeding. As the trellis metaphor caused a lot of misinterpretations (e.g., by Howells 1959, 1993) and vehement criticism from cladists and "splitters," we will come back to this controversy later (see below).

Fourth Case: Delayed Awakening

It is widely known that during the Third Reich, German physical anthropologists were strongly involved in the functioning and ideological underpinning of the Nazi

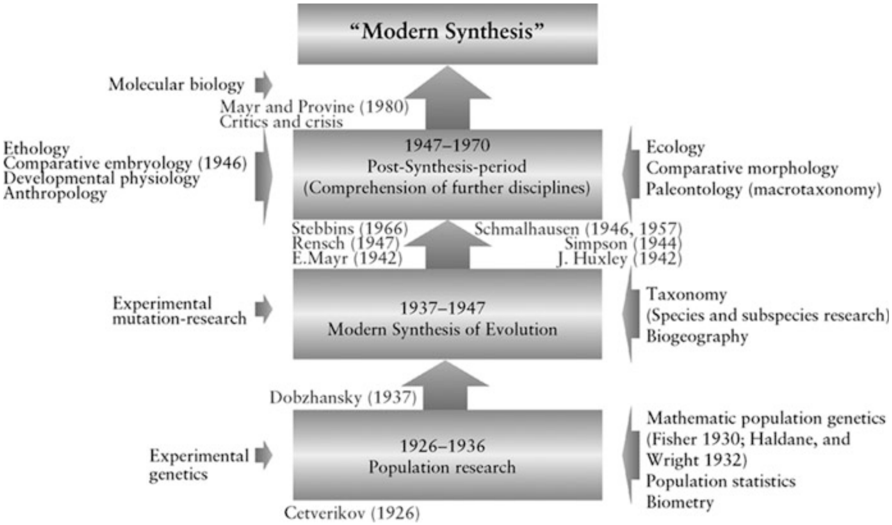


Fig. 8 Development of the theoretical basis of the biological sciences (After Jahn 2000, modified)

regime. In an oppressive manner, e.g., Schafft's (2004) historical analysis "From Racism to Genocide" reveals anthropology's entanglements and unmasks blatant cases of pseudoscience. Therefore, it is not surprising that paleoanthropology was also fraught with racist ideology, though on the international level, there was groundbreaking change in evolutionary thinking (Junker 2004; Hoßfeld 2005b; Mayr 1988). The protagonist of evolutionary thinking, Ernst Mayr (1904–2005), a trained German zoologist, left his homeland in the year 1931 and did his research at the AMNH in New York and after 1953 at the Harvard University in Cambridge. He denied that the "Synthesis" (see Fig. 8) was a revolution; his conclusion was: "It was not so much the discovery of new facts that characterized the synthesis as the removal of misunderstandings. The period from 1859 to 1935 had suffered from being dominated by erroneous conceptualizations, such as essentialism (typology), a belief in an intrinsic tendency toward progress, a misunderstanding of the nature of inheritance and of mutation, a failure to understand the nature of populations and the uniqueness of individuals, and of other erroneous concepts" (Mayr 1988). When misunderstanding of evolutionary principles was commonplace, no wonder German paleoanthropologists didn't conduct acknowledged science. Above all, it must be stressed in this context that the "misunderstandings" mentioned by Mayr in no way equate with wrong conceptions of racial and political ideologies that so horribly became virulent during the era of National Socialism in Germany; there is no excuse for racial discrimination and all kinds of racism from a false understanding of the principles of human evolution. Further, there is absolutely no doubt that a large part of anthropologists and human geneticists were involved in such racist activities, in some cases perhaps only passive, but in many demonstrable cases highly actively, in roles ranging from deskworkers (“Schreibtischtäter”) to racist executioners (Stocking 1988; Proctor 1988; Weingart et al. 1988; Massin 1993, 1996; Hoßfeld 2005b; Schafft 2004).

From the perspectives of paleoanthropology and the history of science, it is noteworthy that during World War II, the first edition of Gerhard Heberer’s compendium “Die Evolution der Organismen” appeared (Heberer 1943). The anthropogenetical contributions of the multifaceted volumes deal, e.g., with comparative anatomy (v. Krogh 1909–1992), paleontology (Gieseler 1900–1976), ethology, and archaeology (Weinert 1887–1967). However, in the view of the scientific historians Hoßfeld and Junker (2003) and Hoßfeld (2005b), the chapter authored by Otto Reche (1879–1966) is the only one that takes the model of synthetic Darwinism into account. I’m in full agreement with the following overall assessment: “. . .[es] handelt sich über weite Strecken um vergleichende Untersuchungen zur Stammesgeschichte der Menschheit, wie sie bereits im 19. Jahrhundert angestellt wurden, ergänzt durch neuere Daten aus Serologie und Paläontologie” (Hoßfeld and Junker 2003, p. 107). Of particular interest, Junker and Hoßfeld (2002, p. 242) mention that the volumes of “Evolution der Organismen” are “with few exceptions – without any reference to national socialist ideas”. The major exception is Heberer’s preface, and the authors assume “that Heberer as editor and the publisher (Gustav Fischer) have demanded ideological neutrality.” The biological impact on paleoanthropology was minor, since in practice fossil discoveries came into the literature through collaboration between the archaeologists who excavated them and the anatomists who described them. Physical anthropologists with a biological background, such as Gerhard Heberer (1901–1973), a convinced national socialist who was induced into the SS by Heinrich Himmler (Deichmann 1995; for biography, see Hoßfeld 1997), were rare (Massin 1993, 1996). These theoretical deficits caused consequences in paleoanthropological thinking, especially concerning Darwinian and Neo-Darwinian thoughts. And I agree with Foley’s (2001, p. 6) statement: “Archaeologists and professors of anatomy seldom made a rich cocktail of Darwinian theory.” In general the descriptive casuistic and more or less narrative approaches in paleoanthropology hold true throughout the period under discussion, and for early postwar times, in Germany as well as in other countries (Tattersall 2000a; Foley 2001; Henke 2010a, b). The period leading up to World War II had seen the emergence of the evolutionary synthesis, but not until the 1950s did innovative biological principles and methods begin to inform paleoanthropological science too (Spencer 1984; Mayr 1988; Delisle 1995; Hoßfeld 1997, 2005b; Jahn 2000; Tattersall 2000a; Foley 2001; Corbey and Roebroeks 2001b; Hoßfeld and Junker 2003; Junker 2004).

What’s the message in all of this? Firstly, research is embedded in an ongoing process of paradigmatic and methodological innovation and needs permanently a critical evaluation. This can most effectively be achieved by international standards. Secondly, physical anthropologists, mainly the negligibly small group of paleoanthropologists in Nazi Germany, missed correctives from outside, or more correctly, many protagonists – like Gerhard Heberer, Wilhelm Gieseler, and Hans Weinert – felt comfortable under a National Socialistic regime in spite of the knowledge of injustice against humanity (e.g., Vogel 1983; Massin 1993, 1996; Hoßfeld 2005a, b). It should also be mentioned that most of them continued their careers in postwar times (Saller 1961; Junker 2004; Preuß et al. 2006; Preuß 2009). Thirdly, every scientist should be aware of the ethical standards of his discipline and should follow ethical rules and the recommendations of good science practice, as personal responsibility will always remain (see Max-Planck-Gesellschaft (1984); AAPA Statement on Biological Aspects of Race (1996) – and ongoing discussion, e.g., Cartmill 1999; Brattain 2007).

Keeping Pace with Other Sciences: Toward a "New Physical Anthropology"

The selected examples given here demonstrate that social and political reasons far removed from paleoanthropology are important; and in this context Dennell (2001, p. 45) reminds us "that paradigmatic shifts in palaeoanthropology occur in response to a wider world, and are not wholly dependent on internal evidence or individual personalities alone."

After World War II, the world opened up, causing drastic changes for paleoanthropology too. Ethnocentricity and old-fashioned typological methodologies of physical anthropology and evolutionary biological thinking were subjected to critical review. The reevaluation of paleoanthropology was mainly carried out by US-American anthropologists like Sherwood Washburn (1911–2000; see Howell 2003; Marks 2000) and especially Francis Clark Howell (1925–2007). His younger colleague Tim White praised him in an obituary (published by Sanders 2007, p. 1, www): "Clark's central importance since the 1950s has been to make paleoanthropology what it is today – that is, the integration of archaeology, geology, biological anthropology, ecology, evolutionary biology, primatology and ethnography." Besides Clark Howell, one must mention the British-born Kenyan Louis S. B. Leakey (1903–1972) (see Isaac and McCown 1976) as a further prominent innovator of the discipline. Desmond Clarke (1976, p. 541) appreciation – by his discoveries, and his brilliant personality, he gained the admiration and captured the imagination of the world – meets it exactly.

In summary, paleoanthropology needs, like all sciences, a properly evaluated underlying theory and methodology (Oeser 2004; Ruse 2005) and can only flourish in open-minded cosmopolitan societies. Furthermore, every discipline needs exceptional personalities too, even if teamwork dominates, and I would like to add, as far as paleoanthropology is concerned, also those with charisma since human evolution is a topic of extreme public interest and with generosity, as "sites" and "nuggets" should be shared according to fair rules (e.g., see EVAN Society, www; NESPOS Organization). These preconditions were developed in the second half of the last century; let's have a closer look at them.

Diversification of Anthropology in the Second Half of the Twentieth Century

Early Post-World War II Period

The principal architects of the evolutionary synthesis mentioned previously gained more and more influence in World War II and postwar times, and their ideas shaped the field of biological anthropology including paleoanthropology (Tattersall 2000a; Foley 2001; Levinton 2001; Mayr 2001; Junker 2004; Hoßfeld 2005b; Wolpoff 2003). Although the fossil record had steadily increased, it was still a challenge to reconstruct the raw outlines of human evolution from the tiny catalog of human skeletal remains. There was tremendous progress as the hominin status (at that time taxonomically termed hominid) of the small-brained, bipedal australopithecines became accepted due to the new finds from fossils from Kromdraai Cave, excavated by Robert Broom (1866–1951) in 1938. The successful excavation of further exciting australopithecine fossils from the cave sites Sterkfontein, Makapansgat, and Swartkrans by Broom and John T. Robinson (1923–2001) after 1947 was the continuation of the success story of human paleontology in South Africa that had started with Dart's description of the Taung child in 1924, had continued with Broom's excavations (Broom and Scheffers 1946), and lasts to the present day (overviews in Grine 1988; Sperber 1990; Partridge et al. 2003; Tobias 2005; Berger et al. 2010; Balter 2011). The diversity of the australopithecine taxa became especially obvious from the megadont *Paranthropus* from Swartkrans, "Another new type of fossil ape-man," as described by Broom (1949, 1952) and Broom and Scheffers (1946). In addition, human origins became even more complex and debatable as the "East Side Story" (sensu Coppens 1994) developed, having started with Wilhelm Kattwinkel's and Hans Reck's explorations in 1911, continued still with scant success by Louis and Mary Leakey in the 1930s, and came into major focus by the discovery of *Zinjanthropus boisei*, a hyperrobust australopithecine (Leakey 1959), and culminated in the successful Afar Research Expedition (Johanson et al. 1978) and many more recent projects.As the dating of known specimens was limited to the relative time scale "older than/younger than," and as the techniques of absolute dating were still unknown (Oakley 1964), there was a lot of uncertainty in the calibrations. The overall picture was a stepwise adaptive evolution from primitiveness to high-order hominids/hominins with modern-shaped bodies and cultural skills. The evolutionary ladder reached from the gracile and robust australopithecines, i.e., very apelike species, to the *Pithecanthropus* and *Sinanthropus* species. These had been lumped with the European *H. heidelbergensis* in a single species, *H. erectus*. This simple gradualistic model regarded the Middle Pleistocene "Java man," "Peking man," and the "Mauer man" as intermediate stages between the early taxa from Africa and the later Neanderthals, a well-documented fossil human group from late Ice Age sites in Europe and western Asia. Little wonder that in this confusion, paleoanthropologists welcomed Mayr's and Dobzhansky's simplifying message that only one kind of hominid (new systematic: hominin) could have existed at any time and that virtually all developments in human evolution since Java man had taken place within the single, albeit variable, species *H. sapiens*. Tattersall (2000a, p. 3) suggests that Dobzhansky was influenced "by his newly arrived New York neighbor Franz Weidenreich, nowadays hailed as the father of 'multiregional continuity'."

Ernst Mayr took the position that at the most three successive species could be discerned within the genus *Homo*: *H. transvaalensis* (the australopithecines), *H. erectus*, and *H. sapiens* (including the Neanderthals). Few paleoanthropologists followed these pronouncements in every detail; however, schemes of hominin evolution routinely came to incorporate the synthesis' basic assumptions, whereby evolutionary change consisted simply of the gradual modification of lineages, usually no more than one, over long spans of time. Human evolution thus became the story of a long, single-minded struggle from primitiveness to perfection which became highly criticized (more later; overview in Tattersall 2000a; see further Foley 2001; Wolpoff 2003). Successively there arose different problems from Mayr's simplified model.

First, the evolutionary model was in contradiction to the mosaic pattern of the erroneously ancient, heavily encephalized Piltdown man. This problem disintegrated when in 1953, Piltdown was declared a hoax by authorities at the British Natural History Museum (Spencer 1990b). Second, paleoanthropological results were severely flawed due to arbitrary taxonomic approaches (see Table 2). For this reason, there was a genuine need for the revision of the overabundance of species and genus names, which had been applied liberally more or less without a taxonomical concept to hominid fossils. The taxonomic revision of the hominid/hominin sample asked for a strict consensus regarding the underlying species concept and how to reconstruct phylogenetic relationships (Washburn 1951, 1953; Hennig 1950, 1966; Remane 1952; Eldredge and Cracraft 1980; Eldredge 1993; Waegele 2000; Gould 2002; Wiesemüller et al. 2003; Lieberman and Vrba 2005; Wood and Lonergan 2008; Henke and Hardt 2011; Willermet 2012). Niles Eldredge's (1993) pressing issue "What, if anything, is a species?" is symptomatic of the need to solve principle taxonomic questions still today (however, this is not an exclusive problem of paleoanthropology; e.g., Hunt 2003). Third, the uncertainty of the temporal allocation of fossils reflected the absence of absolute dating techniques (Oakley 1964; Bishop and Miller 1972). In sum, it became more and more obvious that there was tremendous need for a new and precise strategy of physical anthropology within the frame of a *revised* Synthetic Theory of Evolution (Cartmill 1990a, b; Bowler 1997; Eldredge 1993; Levinton 2001; Tattersall 2000a, b; Lieberman and Vrba 2005; Willermet 2012).

In the immediate postwar period, there arose a body of theory that swept away a host of conflicting notions about the nature of the evolutionary process. The elegantly simple concept stated that all evolutionary phenomena could be ascribed to a single mechanism: the gradual change of genes and gene frequencies within lineages of organisms under the guiding hand of natural selection (Cartmill 1990a, b). Though the innovative population genetic approaches in the 1920s of Ronald A. Fisher (1890–1962), John B. S. Haldane (1892–1964), and Sewall G. Wright (1889–1988) were obviously of great importance for the field of paleoanthropology

Table 2 Hominin taxonomy: Genera and species designations of former and current taxa, temporal and geographical ranges. Except *Homo sapiens*, all the other taxa are extinct (Adapted from Collard (2002), modified and enlarged; see further Groves (2001); Henke (2003b); Wood and Lonergan (2008))

Genus *Homo* Linnaeus, 1758 [including the following genera: *Anthropopithecus* Dubois, 1892, *Pithecanthropus* Dubois, 1894; *Protanthropus* Haeckel, 1895; *Sinanthropus* Black, 1927; *Cyphanthropus* Pycraft, 1928; *Meganthropus* Weidenreich, 1945; *Atlanthropus* Arambourg, 1954; *Telanthropus* Broom and Robinson, 1949; earliest appearance in the Pliocene, worldwide distribution]
Homo sapiens Linnaeus, 1758. Pleistocene to present, worldwide
Homo neanderthalensis King, 1864. Pleistocene, Europe, Western Asia, Siberia, Near East
Homo erectus (Dubois, 1892), Weidenreich, 1940. Pleistocene, Asia, (Europe?, Africa ?)
Homo heidelbergensis Schoetensack, 1908. Pleistocene, Africa and Europe
Homo rhodesiensis (cf. *heidelbergensis*) Woodward 1921. Pleistocene, Africa
Homo helmei Dreyer, 1935. Pleistocene, northern and East Africa
Homo soloensis Dubois, 1940. Middle Pleistocene, Southeast Asia
Homo modjokertensis v. Königswald, 1950. Early Pleistocene, Indonesia
Homo mauritanicus Arambourg, 1963. Middle Pleistocene, Northwest Africa
Homo habilis L.S.B. Leakey et al., 1964. Plio-Pleistocene, Africa
Homo ergaster Groves and Mazák, 1975. Pleistocene, Africa and Eurasia
Homo palaeojavanicus Sartono, 1981. Middle Pleistocene. Southeast Asia
Homo rudolfensis (Alexeev, 1986), Wood 1992. Plio-Pleistocene. East Africa and Malawi
Homo antecessor Bermudez de Castro et al., 1997. Early Pleistocene, Western Europe
Homo georgicus Gabunia et al., 2002. Early Pleistocene, Northwestern Asia
Homo cepranensis Mallegni et al., 2003. Early Pleistocene, Italy
Homo floresiensis Brown et al., 2004. Late Pleistocene–Early Holocene, Indonesia [“Denisova Man,” sometimes designated as “Homo denisovan” is not regarded as a species by Krause et al. (2007, 2010)]
Genus *Australopithecus* Dart, 1925 [includes the genus *Plesianthropus* Broom, 1938]. Pliocene, Africa
Australopithecus africanus Dart, 1925. ca. 3.0–2.5 Ma; South Africa
Australopithecus afarensis s.s. Johanson et al., 1978. ca. 3.7–3.0 Ma; Ethiopia, Tanzania, Kenya
Australopithecus anamensis M.G. Leakey et al., 1995. ca. 4.2–4.0 Ma; Kenya
Australopithecus bahrelghazali Brunet et al., 1996. ca. 3.5–3 Ma; Tchad (North Africa)
Australopithecus garhi Asfaw et al., 1999. ca. 2.5 Ma; Ethiopia
Australopithecus sediba Berger et al., 2010. ca 1.78–1.95; South Africa
Genus *Paranthropus* Broom, 1938 [includes *Zinjanthropus* L.S.B. Leakey 1959, *Paraustralopithecus* Arambourg and Coppens, 1967]. Plio-Pleistocene, Africa
Paranthropus robustus Broom, 1938. ca. 1.5–2.0 Ma; South Africa
Paranthropus boisei L.S.B. Leakey, 1959. ca. 2.3–1.4 Ma; Tanzania, Kenya, Ethiopia, Malawi
Paranthropus aethiopicus Arambourg and Coppens, 1968. ca. 2.7–2.3 Ma; Ethiopia, Kenya, Tanzania (?)
Genus *Ardipithecus* White et al., 1994. Pliocene, East Africa
Ardipithecus ramidus s.s. White et al., 1994. ca. 4.5–4.3 Ma, Ethiopia
Ardipithecus kadabba Haile-Selassi et al., 2004. ca. 5.8–5.2 Ma, Ethiopia
Genus *Kenyanthropus* M.G. Leakey et al., 2001. Pliocene, East Africa
Kenyanthropus platyops M.G. Leakey et al., 2001. ca. 3.5–3.3 Ma, Kenya

(*continued*)

Table 2 (continued)

Genus *Orrorin* Senut et al., 2001. Miocene, East Africa
Orrorin tugenensis Senut et al., 2001. 6.6–5.7 Ma, Tugen Hills, Kenya
Genus *Sahelanthropus* Brunet et al., 2002. Miocene, northern East Africa
Sahelanthropus tchadensis Brunet et al., 2002. ca. 7–6 Ma, Tchad

too, and notwithstanding that the protagonists of the *Synthetic Theory of Evolution* had given special attention to this area at the time when the discipline was absorbing its theoretical underpinnings, there was need for active initiatives by (paleo-) anthropologists themselves. First, the rejection of the typological approach was required before population genetic thinking could board the New Physical Anthropology sensu Washburn in the 1950s. However, many challenges had to be overcome, and some are still waiting to the present day (Vogel 1983; Foley 1987; Martin 1990; Delisle 1995; Wolpoff 1999; Tattersall 1995, 2000a, b; Foley 2001; Levinton 2001; Gould 2002; Jobling et al. 2004; Cartmill and Smith 2009; Fuentes 2010).

New Strategies, Concepts, and Challenges in Physical Anthropology

In the early 1950s, there began an intensive discussion on the strategy of physical anthropology, i.e., the body of scientific theory and techniques with which it attacks its problems. Washburn (1951, 1953) was one of the protagonists of a new conception which was formulated in the new version shown in Fig. 9. The main step was to reduce the speculative and narrative part of physical anthropology in favor of thorough hypothesis testing. Cartmill (1990b, p. 189) puts it this way: “No doubt, people are different from the apes; but it is our job as scientists to explain those differences. Explanation, as opposed to mere storytelling, has to invoke law-like regularities connecting causes and effects.” This then was the challenge facing the evolutionary biological sciences (Popper 1968). Of greatest importance for the renewal of physical anthropology were the rejection of typological concepts and an increased interrelationship between the different parts of anthropology. The change from descriptive studies to the investigation of process and behavior brought about the integration of the problems of human evolution in the vast scientific field of mammalian evolutionary biology. Solutions to problems consequently followed, on the one hand, from paleontology, primatology, genetics, population genetics, ecology, and diverse medical sciences and, on the other hand, from the study of archaeology and ethnology.

The great challenge of human evolutionary biology became the cultural factor, as adaptations, human migrations, mating systems, population densities, diseases, and human ecology all became factors seen as essential to the explanation of our special human way of life (Washburn 1953; Vogel 1966; Osche 1983; Foley 1987, 2010; Tattersall 1995, 1998, 2002, 2012; Wolpoff 1996–97; Cartmill and Smith 2009; Foley and Gamble 2009; overviews in Henke and Rothe 1994;

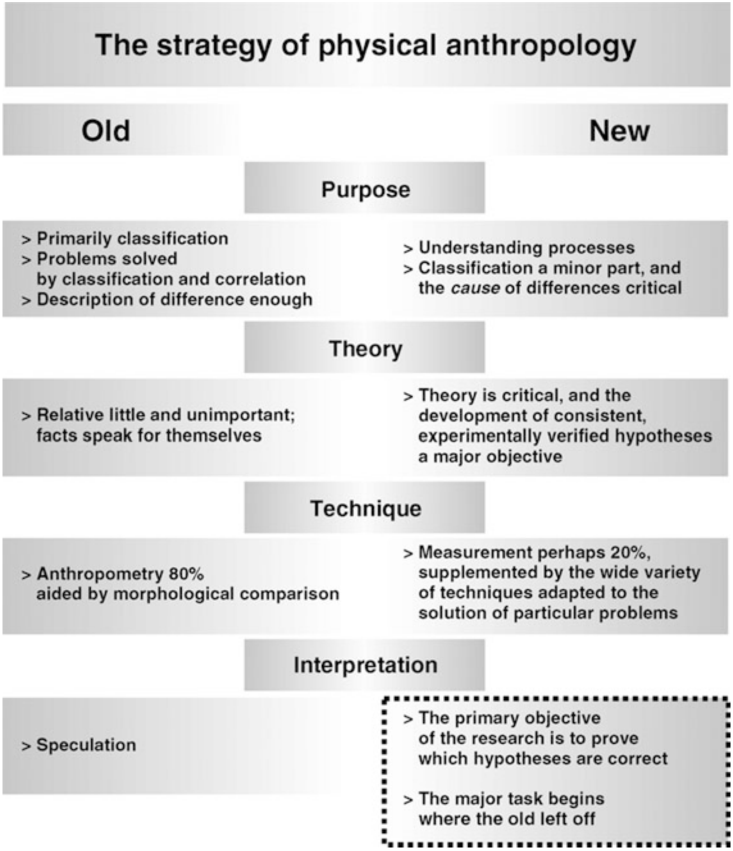


Fig. 9 The strategy of physical anthropology (Redrawn from S.L. Washburn 1953, modified)

Delson et al. 2000; Wood 2011; Begun 2013). Washburn's (1953, p. 726) prognosis was: "If we would understand the process of human evolution, we need a modern dynamic biology and a deep appreciation of the history and functioning of culture. It is this necessity which gives all anthropology unity as a science."

The recognizable post-World War II shape of paleoanthropology resulted from the belated acceptance of neo-Darwinian principles of evolutionary biology, which were successively brought together in the 1930s and 1940s and unified evolutionary biology under a single roof, sweeping away a huge package of mythological narrative thinking (Henke and Rothe 2006; Goodrum 2009). Delisle (1995, p. 217) suggested "that the evolutionary synthesis directly influenced on human paleontology [during the decade 1950–1960] every day practitioners in human paleontology almost solely through the general concepts and methods of the new systematics. Instead of being only a common core shared by a host of disciplines, the evolutionary synthesis should also be defined by the extent to which that core has been guiding current research in any one field."

Washburn's concept of a *New Physical Anthropology* was received with enthusiasm by the scientific community, and the impetus for the development of the individual subdisciplines has been tremendous (see Fuentes 2010; Lille and Kennedy 2010; Larsen 2010), though not by all, e.g., the German anthropologists who slumbered through the theory change (see Vogel 1983; Henke and Rothe 1994, 2006). Despite its generally positive reception, vehement critics have appeared since the 1970s, as it was asked: Was the Modern Synthesis a real step forward in the right direction? The dispute over *evolutionary theory* opened with a stimulating paper on "Punctuated equilibria: an alternative to phyletic gradualism" by Niles Eldredge and Stephen J Gould (1972), originally presented at the *Annual Meeting of the Geological Society of America* in 1971. This was an astonishing contribution, though not entirely unexpected as other evolutionary models, e.g., Weidenreich's "trellis" (Fig. 7), had been under heavy criticism for a long time (see Howells 1959; overviews in Shipman 1994; Wolpoff and Caspari 1997). Gould and Eldredge contrasted the hypothesis of "punctuated equilibria" [which proposes that evolutionary changes occur in geologically rapid events of branching speciation called cladogenesis] against the hypothesis of "phyletic gradualism" [which assumes that evolution generally occurs by anagenesis, uniformly, and by the steady and gradual transformation of whole lineages]. Interesting enough, that research on the evolution of Paleozoic invertebrates had guided Eldredge (1971) to the suggestion that allopatric speciation might be the resolution instead of gradual evolution. His enlightening idea that the pattern of descent is marked by long periods of stasis alternating with rapid changes caused great evolutionary debate (e.g., Wolpoff 1971, 1980, 1996–1997; Eldredge and Gould 1972; Gould and Eldredge 1977; Gould 2007; Tattersall 1994, 1998, 1999, 2000a, 2002; Eldredge 1995; Wolpoff and Caspari 1997; Foley 2001; Cartmill and Smith 2011).

Eldredge's (1995) review of the history of the twentieth-century evolutionary theory is entitled "Reinventing Darwin" and deals from an insider perspective with the confrontation of the "Ultra-Darwinians" and the "naturalists," whose disputes were not always collegial and unpolemic (see, e.g., Wolpoff and Caspari 1997). Those who want to know more about "The Growth of Paleobiology as an Evolutionary Discipline" should read David Sepkoski's (2012) "Rereading the Fossil Record"; we will concentrate here solely on the history of paleoanthropology as a subdiscipline of paleobiology.

Just at the time when the "reinvention" by Gould and Eldredge started, Ian Tattersall had finished his thesis on "Subfossil Lemurs of Madagascar" at Yale University. Inspired by his own research on the vast diversity and variability of the lemurs in combination with the burgeoning (*re*-)evolutionary views in the 1970s, he started an extremely fruitful cooperation with Niles Eldredge, whose colleague he became at the AMNH in New York (e.g., Eldredge and Tattersall 1982). Reviewing the last half-century, Tattersall (2000a, p. 2) reaches the following crushing conclusions about the influence of the Dobzhansky et al.'s "Synthesis": "Sadly, however, the Synthesis was doomed to harden, much like a religion, into a dogma: a dogma whose heavy hand continues to oppress the science of human origins a half-century later." Tattersall (2000a, p. 5) complains that paleoanthropology was laggardly "Slow to absorb the principles of the Synthesis, palaeoanthropology has been equally slow to augment these principles with recognition of the multifarious complexities of the evolutionary process." He gives many convincing arguments for this judgment, e.g., Dobzhansky's lumping of the fossil hominids, with the conclusion "that there existed no more than a single hominid species at any one time level" (Dobzhansky 1944, pp. 261–262). Furthermore, he criticizes Mayr's claim that humans did not speciate (Mayr 1950), a position which opened for Weidenreich and later proponents the so-called single species hypothesis which mainly "rests on the nature of the primary hominid adaptation: culture (structured learned behaviour). Because of cultural adaptation all hominid species occupy the same, extremely broad, adaptive niche. For this reason, allopatric homind species would become sympatric. Thus the competitive exclusion principle can be legitimately applied. The most likely outcome is the continued survival of only one hominid lineage" (Wolpoff 1971, p. 601).

It became very soon evident that the controversial positions of "lumpers" versus "splitters" would lead to sharp disputes in paleoanthropology; and when the long-unsolved Neanderthal problem (overviews in Trinkaus 1989; Vandermeersch 2002; Bar Yosef and Vandermeersch 1991; Stringer and Gamble 1993; Trinkaus and Shipman 1993; Wolpoff 1999; Clark and Willermet 1997; Tattersall 1999; Henke and Rothe 1999b; Harvati and Harrison 2006; Vandermeersch and Maureille 2007; Cartmill and Smith 2009) merged into the controversy of "multiregionalists" versus "replacement proponents," the big paleoanthropological issue of the last four decades was on the floor. An almost endless series of conferences, congresses, scientific papers, proceedings, readers, and last but not least popular science media has addressed this topic.

It was shown above that the controversy of proponents of "unilinearism" versus "multiple species concepts" smoldered long before the 1970s, when William W. Howells (1908–2005) had interpreted Weidenreich's view as the "Candelabra Hypothesis" (Howells 1959). Other prominent anthropologists joined Howells, in spite of the fact that this characterization didn't match Weidenreich's original statement. The hot debate started when the British paleoanthropologist Christopher Stringer (1974) presented the results of his thesis on "Population Relationships in Later Pleistocene Hominids: A Multivariate Study on Available Crania." His *Out of Africa* model claimed – in a late version – a *total replacement* of the non-African archaic populations. Very similar to Stringer's *Recent African Origin* model (RAO I) was Günter Bräuer's "Afro-European *sapiens* hypothesis" (Bräuer 1984; RAO II). The habilitation thesis of the German anthropologist was based on a sophisticated morphological comparison of a broad cranial dataset, taking revised calibrations of the Middle Stone Age in Africa into account. In spite of many similarities between the models, there was a significant difference: Bräuer's hypothesis assumes degrees of "hybridization" between modern and archaic humans (including the Neanderthals). Smith and Cartmill (2009, p. 473) summarize: "Bräuer's model thus has strong flavor of replacement – if not so of species, at least of local populations." The opposing *Multiregional theory* (MRE) by Wolpoff (1971, 2004) was – in some essential aspects – confronted by a further theory within the bundle of continuity and replacement hypotheses in *Homo sapiens* evolution, the so-called Assimilation Model (AM) proposed by Smith et al. (1989). Like the MRE, the AM too recognizes important gene flow between archaic and modern human populations in Eurasia. Concerning the Neanderthals, the AM rejects separate species status, and this is assumed for other Middle and Late Pleistocene populations too (Cartmill and Smith 2009, p. 473).

If we follow the history of the “continuity or replacement” discussion in some prominent contributions, we have to admit that something must have gone wrong (see, e.g., Andrews and Franzen (1984), Smith and Spencer (1984), Wood et al. (1986), Giacobini (1989), Mellars and Stringer (1989), Smith et al. (1989), Trinkaus 1989; Bräuer and Smith (1992), Aitken et al. (1993), Frayer et al. (1993); Meikle et al. (1996), Clark and Willemet (1997), Tobias et al. (2001), Crow (2002), Barham and Mitchell (2008), Condemi and Weniger (2011)). Why was everybody trying to verify their own hypothesis, when falsification should be the method of choice? Why was it apparently so difficult to gain consensus on the underpinning theory and methodology? What made it so difficult to exclude the one or the other model by falsification? Next to these and many other scientific questions, there is a personal one: Why often so emotional? Scientists are not married to their scientific statements; they can “divorce” and admit when they were wrong.

All this begs the question: Is paleoanthropology really a discipline apart from the mainstream of biological thinking, and has the Modern Synthesis really shadowed the scientific work of paleoanthropologists? During the last 50 years, the vestiges of the so-called step ladder model have been successfully refuted [no wonder, when we consider the increased fossil record and the flood of hominin taxa in the Mio-Plio-Pleistocene which can’t be ignored; see Table 2]. While the unilinear and chiefly anagenetic models vanished from the discussion [almost], it became increasingly obvious that the process of human evolution is convincingly represented by multiple species, cladogenesis, and adaptive radiations [when looking at the Mio-Pliocene] as well as by the processes of the punctuated equilibrium model. But, what has happened to the genus *Homo*? (see Henke and Hardt 2011).

However, is this “mainstream” thinking on RAO in current paleoanthropology illusory, insofar as some of the opponents have thrown in the towel? It would be of great interest to know, via a scientific historic approach, which factors have played the decisive role: purely convincing scientific arguments or personal dynamics within the scientific community (coalitions and alliances)? And what about all the publicity and media attention? Paleoanthropology isn’t, and never was, operating in an ivory tower. What is the role of “embedded” scientific journalists in the acceptance or rejection of results of paleoanthropological research? Is anthropology, as a media-friendly subject, particularly at risk? (See Franck 1997, 1998a, b; Stoczkowski 2002; Grim 2009).

Was the Modern Synthesis really an obsolete theory which was uncritically used to give support for unilinearism? (Tattersall 1998, 2000a). Foley’s less negative comment on this centers on the point that paleoanthropology remained “in fact [. . .] blithely innocent of most theoretical issues.” Foley emphasizes that "anthropologists undoubtedly read the modern synthesis as suggesting that there can be no cladogenesis, but rather than seeing the true nature of Darwinian theory they merely saw their own theoretical reflecting" (Foley 2001, p. 5–9).

Foley's opinion that anthropology of the last half-century had many theoretical deficits agrees with that of my academic supervisor Christian Vogel (1933–1994), the former head of the Institute of Anthropology in Göttingen. Vogel had formulated the "biological perspectives of anthropology and the so-called theory-deficit of the physical anthropology in Germany," quoting Washburn (1953), who pleaded that the "application of a constituent, experimentally verified, evolutionary theory is the first task of the physical anthropologist" (Vogel 1983, p. 225). One should remember that Vogel's paper was presented in 1981, reflecting that paleoanthropology, and in a wider sense physical anthropology, remained behind the other evolutionary sciences (Spiegel-Rösing and Schwidetzky 1982). Although paleoanthropology was not the foremost field of anthropological research in Germany, new editions appeared of *Die Evolution der Organismen* (Heberer 1959, 1967–1974) and the textbook *Menschliche Abstammungslehre* (Heberer 1965a). In spite of these and other prominent publications in Germany in the 1960s and 1970s (Kurth 1962, 1968; Heberer 1968b; Hofer and Altner 1972; Kurth and Eibl-Eibesfeldt 1975; overviews in Hoßfeld 1997, 2005a, b; Henke and Rothe 2006), there remained a theoretical vacuum in anthropology, and paleoanthropology seemed here – as well as in other European countries – much more fossil driven than hypothesis guided.

A further appeal came from Cartmill (1990a, b, p. 173) who claimed in the early 1990s that: "Paleoanthropology should aim at increasing its theoretical content by reducing the list of qualitative human uniquenesses-and eliminating it altogether if possible." The evaluation of the scientific reasons that perpetuated inadequate evolutionary approaches in paleoanthropology, and caused complacency with insufficient models, is still incomplete. Whether "the Synthesis was doomed to harden much like a religion, into a dogma", as Tattersall claims (2000a, p. 2; contra Foley 2001), is a continuing issue; but most can agree with the statement that paleoanthropology was not explicitly theoretical, but was descriptive and in part excessively narrative (Bowler 1996, 2001; Foley 2001; Stoczkowski 2002; Ickerodt 2005; Henke 2007b, 2010a; Henke und Herrgen 2012).

In contrast to the European situation, paleoanthropologists in the USA have traditionally been trained as physical and cultural anthropologists (see Lille and Kennedy 2010). This caused a different approach to research in human evolution; in the traditional European system, archaeologists as a rule dug up the fossils, and they or anatomists – not physical anthropologists – described them and perpetuated the problem. The simplicity of narrative approaches also hampered progress. The idea of human uniqueness was emphasized (Cartmill 1990a, b), and hominin fossils were treated casuistically. Foley (2001, p. 7) confesses that it was "frustration with the combination of an absence of evolutionary theory in human evolution and assumptions about human uniqueness that led me to write Another Unique Species (Foley 1987)." His sophisticated approach tries to explain the process of human evolution and the human adaptive strategy as the intersection of the biological categories to which hominins (in Foley's original hominids) belong (Fig. 10).

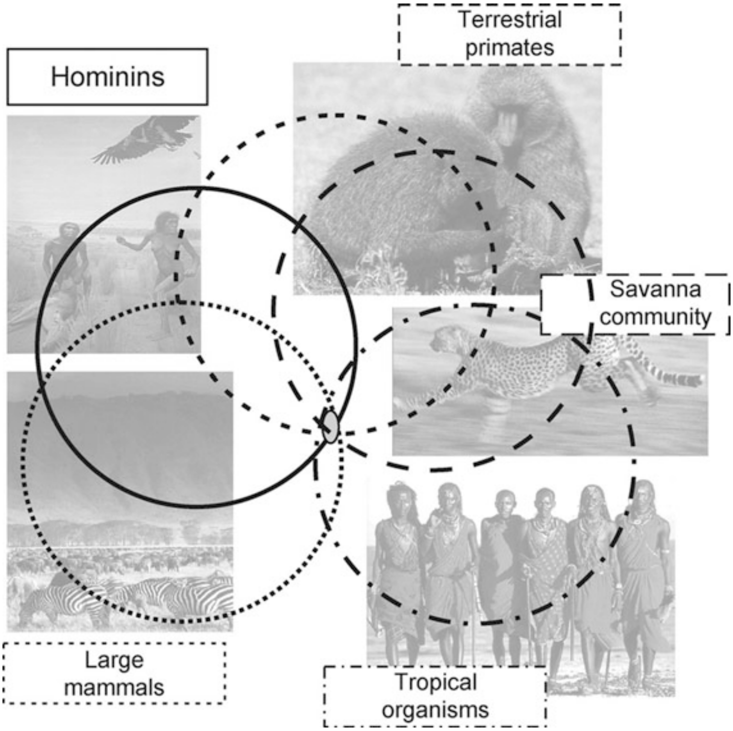


Fig. 10 Venn diagram of human uniqueness and the human adaptive strategy as the intersection of the biological categories to which hominins belong (After Foley 1987, modified)

Although most hominin diversity can be explained by evolutionary changes caused by geographical-climatological factors, there is a vast explanatory field within the life sciences, particularly comparative primatology, sociobiology, paleoecology, and paleogenetics. The multidisciplinarity of paleoanthropology is demonstrated in Fig. 11, but without a detailed special ranking of the importance of the cooperating disciplines. The preference for cooperation naturally depends on the paleoanthropological problems that have to be solved, but it should be remembered that inter-, multi-, and transdisciplinarity is a learning process, and an everlasting challenge for science (Mittelstraß 1989; Drilling 1992; Eggert 1995; Porr 1998; Henke and Rothe 2003; Henke and Herrgen 2012).

The Human Career: Revised

How Many Hominin Species Have There Been?

The last half-century has witnessed a dramatic improvement in our understanding of the process of human evolution, due to new approaches and techniques as well as a tremendous increase in the fossil record (Andrews and Franzen 1984; Franzen 1994;

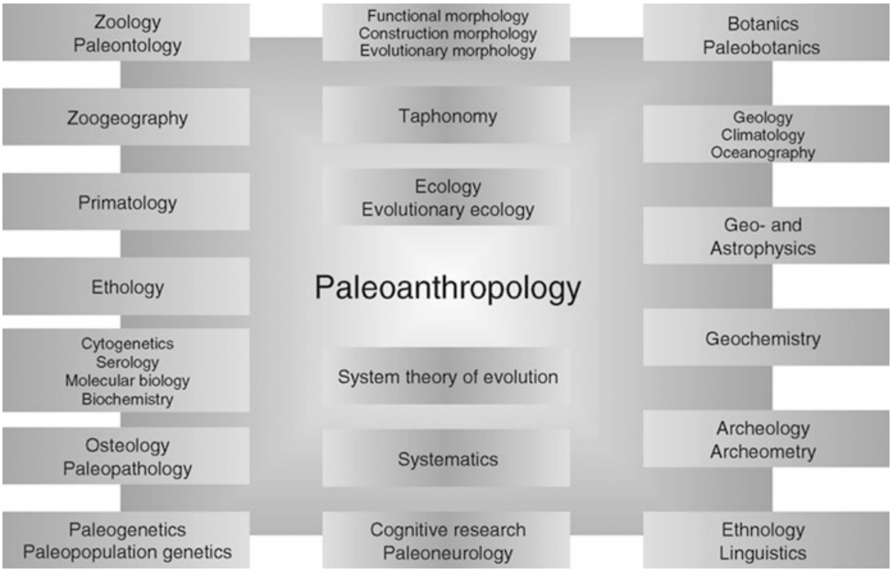


Fig. 11 Scientific disciplines that participate in reconstructing the process of human evolution (After Henke and Rothe 1994)

Henke and Rothe 1994; Ullrich 1995, 1999; Johanson and Edgar 1996; Hartwig 2002; Schwartz and Tattersall 2002, 2003, 2005; Cartmill and Smith 2009; Wood 2011; Begun 2013). Profound knowledge of the relationship between form and function has come from innovations in mechanical engineering, light microscopy and REM, and 2D and 3D tomography, as well as from innovative approaches in geometric morphometrics (Grupe and Peters 2003; Zollikofer and Ponce de León 2005; Bose 2013). Furthermore, evolutionary and developmental morphology (Minugh-Purvis and McNamara 2002) and primate physiology (Martin 1990) have contributed to a better understanding of form-function complexes (Ciochon and Corrucccini 1983; Oxnard 1984; Aiello and Dean 1990; Anapol et al. 2004; Ross and Kay 2004; Slice 2005). Hennig's *Phylogenetic Systematics* (Hennig 1966, 1982, 1984), which was first published in German in 1950 without gaining much attention (Hennig 1950), eventually revolutionized phylogenetic discussion in concert with tremendously increased skills in taxonomy and computer techniques (Rieppel 1999; Waegele 2000; Wiesemüller et al. 2003). In spite of all the positive aspects of innovative methodological approaches, paleoanthropologists shouldn't forget that all sophisticated quantitative approaches in taxonomy are used on extremely small fossil samples and limited datasets. In the context of taxonomy, Tim White (2000, p. 29) warned: "Hennig was not God, and parsimony is not God's truth." Wood and Lonergan (2008, p. 374) put it this way, and advised practitioners of paleoanthropology "to apply a healthy dose of skepticism to pronouncements about the taxonomy and systematics of the human clade." A corrective to the "taxon federation" is Robert B. Eckardt's (2000) textbook

Human Paleobiology. His “attitude to the past” soundly criticizes “splitting” and calls for a check on it. Eckardt’s concept was highly influenced by Paul T. Baker (1927–2007), whose major field of research was human adaptability (“Man Must Adapt, or Be Damned,” Baker 1983). And his paleobiological approach embodies the “endeavor to reconstruct credible impressions of past populations and their members as they were in life: feeding; mating; giving birth to offspring and caring for them; avoiding predators; and enduring vagaries of weather, parasites, and diseases,” (Eckardt 2000, p. 1) a concept very near to Foley’s (1987, 1995a, b) and that of Henke and Rothe (1994, 1999a).

With the improvement of absolute dating techniques (e.g., radiocarbon and other isotopic calibrations) and in relative dating by faunal complexes, the chronological pattern of human evolution was more precisely observed, and it became seen through the application of “molecular clocks” that the branching of the hominin line coincided with the aridification of the East African Rift Valley (Bishop and Miller 1972; Howell 1978; Vrba et al. 1995; Magori et al. 1996; Bromage and Schrenk 1999; Bobé and Behrensmeyer 2004). This allowed for a more effective exploration of hominin sites, increasing the chances of finding fossils of Mio-Plio-Pleistocene faunal complexes. However, as hominins are comparatively rare animals, it still needs much luck to find them. To increase the chances of doing so, taphonomy, the science of decay of organisms and the process of fossilization, first described in 1940 by Efremov, has become an important subdiscipline. Phenomena of biostratinomy, decomposition, and diagenesis are essential for the interpretation of fossils (Behrensmeyer and Hill 1980; Shipman 1981; Etter 1994; Vrba et al. 1995; Martin 1999; Wagner 2007).

The more research on human evolution concentrated on the African continent, the more successful those paleoanthropologists with a licence to dig became, especially as they extended their campaigns into the Miocene as well as to Plio- and Pleistocene strata. Louis Leakey’s good fortune (Cole 1975; Isaac and McCown 1976) at Olduvai Gorge [discovered by the German neurologist Wilhelm Kattwinkel in 1911 (Glowatzki 1979) and successfully explored for the first time in 1913 by Reck (1925)], as well as that of his family members at Koobi Fora and diverse other East African sites, resulted from tremendous efforts (Leakey and Leakey 1978; Grine 1988; Wood 1991; Tobias 1991; Walker and Leakey 1993). Besides the activities of the Leakey family, there should be mentioned the successful expeditions of Francis Clark Howell in Omo, Glynn Isaac in Olorgesailie, and of course the famous Afar Research Expedition (Johanson and Edey 1980; Johanson and Edgar 1996). Finally, the Hominid Corridor Research Project of Timothy Bromage and Friedemann Schrenk in Malawi (Bromage and Schrenk 1999; Schrenk and Bromage 2002) must be alluded to, as well as the activities of Brigitte Senut and Martin Pickford in Tanzania (Pickford and Senut 2001) and Michel Brunet et al. (2002) in Chad. Many findings had to be corrected due to new research, and Pickford’s (1997) “Beyond the Evidence” demonstrates that forcefully.

In the last decades, there have been impressive discoveries of early hominins in South African, at new sites, by Ron Clarke, Lee Berger, and colleagues. Africa has become the “Mecca” of paleoanthropologists. There is no longer any doubt now that Africa was the “cradle of mankind.” The hominin taxonomy presented in Table 2 presents the current list of species recognized by “splitters.”

In spite of the fact that the “fossil hunting” has mostly been done in Africa, many activities in other parts of the Old World allow us to learn more about patterns of hominid migration and development. Exciting new fossils and findings from, e.g., Atapuerca (Spain) (Arsuaga et al. 1999), Apidima (Greece) (Pitsios 1999), Ceprano (Italy) (Ascenzi et al. 2000), Schöningen (Thieme 1996), Dmanisi (Georgia) (Bräuer et al. 1995; Henke et al. 1995; Gabunia et al. 1999a, b, 2000, 2002; Vekua et al. 2002; Lordkipanidze and Vekua 2006), and many non-European and Eurasian sites (Delson 1985; Rightmire 1990; Franzen 1994; Johanson and Edgar 1996; Delson et al. 2000; Brunet et al. 2002; Schwartz and Tattersall 2002; Harvati and Harrison 2006), and the astonishing fossils from Flores (Indonesia) (Brown et al. 2004; Aiello 2010; Falk 2011) demonstrate that paleoanthropology is a field of research with never-ending surprises and new perspectives, albeit with never-ending problems. To say that the sample is too scarce is indeed right when we compare the fossil record with the assumed size of paleopopulations, and how about the number of recognized taxa? Foley asked in 1991, “How many hominid species should there be?” and again 15 years later, when there were claims of 28 hominin species (Foley 1991, 2005). Through highly elaborate comparative modeling, Foley concluded among other things that “it can be seen that the rate of discovery has rapidly increased in the last half-century, and there is no sign of an asymptote. To this extent, it may be proposed that we are still underestimating the number of hominin species” (Foley 2005, p. 69). This may have been a shock for “lumpers,” but some sentences later he says: “In considering the extent to which our knowledge of hominin evolutionary diversity is a challenge to how confident we are that the pattern is ‘real’, we come away with the conclusion of moderate confidence” (Foley 2005, p. 69). While we may underestimate the number of hominin species in the earlier periods, the “full diversity is not yet known even for later periods. What is almost certainly not the case is that we are overestimating diversity” (Foley 2005, p. 70). Good news for excavators and for laboratory scientists too.

However, new fossils are not only solving problems but are raising new questions and providing new answers to that had seemed to have been solved. Here I mention two outstanding cases, both, interestingly enough, from Asia: One of the best illustrations of the phrase “humans are animals who wonder intensively and endlessly about their origin” is partial skeletons of nine hominin fossils (including one complete cranium) from Flores (Indonesia). The “Flores Man” represents a – possible – new species, *Homo floresiensis* (Brown et al. 2004). The most complete individual from the Liang Bua Cave, LB1, was nicknamed the “hobbit” due to its extremely small body size (106 cm) and cranial capacity (380 cc). The unusual anatomy of the fossils caused vehement discussion (e.g., on microcephaly, Laron syndrome, congenital hypothyroidism), and some skeptics regarded LB1 and LB6 as cretins; however, the pathological diagnoses have been largely falsified (Falk et al. 2007; contra, e.g., Martin et al. 2006). Given the case that genetic mutations, diseases, and growth disorders do not apply, the Flores hominins are most reasonably (or better: plausibly) explained as “Late-surviving species of early *Homo*”

(5-year overview of *H. floresiensis* research in Aiello 2010). Public interest was unbelievably intensive due to the striking features of the fossils, and the unusual archaeology of the site, as well as to the diagnostic controversies and claimed skullduggery – a godsend for public media.

Enormous scientific interest, and huge media hype, brought the tiny fossil remains from the Denisova Cave (southern Siberia) to fame. Paleogenetic research using DNA extracted from a finger bone revealed that this individual was from a group (hominin form) that shared a common origin with Neanderthals. Reich et al. (2010, abstract) conclude that "this population was not involved in the putative gene flow from Neanderthals into Eurasians; however, the data suggest that it contributed 4–6 % of the genetic material to the genomes of present-day Melanesians." The authors suggest that the "Denisovans" may have been a widespread hominin population in Asia during the Late Pleistocene. The morphology of a single tooth, whose mitochondrial genome resembles that of the finger bone, suggests an evolutionary history apart from both Neanderthals and modern humans (Gibbons 2011). The floor is wide open for discussion! Or, to put it in Jonathan Marks' words: "Fossil genomics is opening new windows to the past. But the view through them isn't as clear as we like to think" (Marks 2012, p. 1).

Our Ancestors' Great Leap Forward: Changing Explanations

No doubt, the half-life of our theoretical models is very short. But there has undoubtedly been enormous progress, on balance. Besides the paleontological fieldwork, which has also produced valuable data for the reconstruction of the ecological niches of our ancestors (Bromage and Schrenk 1999), research in primatology has become increasingly important for anthropological modeling (Martin 1990; MacPhee 1993; Fleagle 1999; Groves 2001). Thanks to Louis Leakey's encouragement, Jane Goodall, Diane Fossey, and Birute Galdikas started their primatological field researches many decades ago. Their results revolutionized our thinking on primate behavior, and this concept has been enlarged by many other field and laboratory primatologists (see, e.g., research projects of Cheney and Seyfarth; Premack, Fouts, Savage-Rumbough, de Waal, and the working groups of the Max Planck Institute of Evolutionary Anthropology in Leipzig, Germany). The paradigm of behavioral ecology and sociobiology has shaped our hypotheses on food choice, foraging patterns and food detection, as well as on food sharing and intra- and intergroup relations.

It must be mentioned briefly that paleoanthropology as a multidisciplinary research field also brings the major events of primate evolution into focus, to disentangle the evolutionary trends in primate evolution, and to detect our *constitutional preadaptation/predisposition* (see Vogel 1975). Weighty volumes have been edited, e.g., by Fleagle and Kay (1994), Delson et al. (2000), Hartwig (2002), Ross and Kay (2004), Wood (2011), and Begun (2013), proving that "the study of anthropoid origins continues to be a lightning rod for research in paleoanthropology" (Ross and Kay 2004, p. vii). As the focus of this overview is foremost on hominins, let's look briefly at the evolution of bipedal walking as the assumed initial step into humanity. Despite the fact that bipedalism has evolved independently multiple times in primates, and this transition is deeply rooted in the primate behavior, in nonhuman contexts, it is merely facultative, not habitual or obligate.

Since Darwin's (1871) *Freeing of the Hands* hypothesis, the emergence of upright posture and bipedal gait has been discussed in many contexts, proposing alternative triggers and constructing alternative scenarios. Here are some of them: *The Infant Carrying* hypothesis by Etkin (1954); *The Watching Out* hypothesis by Dart (1959); The *Aquatic Ape* hypothesis, initiated by Alister Hardy (1960), presented in detail by Elaine Morgan (see 1997); *The Carrying Food or Provisioning* hypothesis by Hewes (1961); *The Reaching for Food* hypothesis by Jolly (1970); *The Orthograde Scrambling* hypothesis by Sugardijto and van Hoff (1986); *The Display Hypothesis* by Chaplin et al. (1993); The *Scavenging Hypothesis* by Blumenschine and Cavallo 1992 [see earlier untested versions by Eiseley (1953) and Bartholomew and Birdsell (1953)]; *The Thermoregulation* hypothesis (Ward and Underwood 1967; Wheeler 1984, 1991a, b); *The Throwing* hypothesis (Kirschmann 1999; Dunsworth et al. 2003; Young 2003); *The Amphibian Generalist Theory* by Niemitz (2002, 2004, 2010); and *The exploitation of retained locomotor behavior* hypothesis (Thorpe et al. 2007).

While some of the hypotheses/theories are based on monocausal explanations (which shouldn't be regarded per se as most parsimonious solutions), others are more complex and multifaceted, taking into account new paleoanthropological findings and biomechanical and energetic aspects of the anatomy of early hominids, as well as ecological and nutritional prerequisites and evolutionary psychological components. Though some proposals of primary "causes and consequences" seem quite *plausible*, it must be remembered that "plausibility" is an inadequate quality criterion to explain derived features (Foley 1987; Foley and Gamble 2009). The fatiguing, and in retrospect almost absurd, discussion on "facts and fiction" in regard to the *Aquatic Ape Theory* (Roede et al.1991) should remind us that it is not necessary to discuss each conceivable proposal in this field (see Stoczkowski 2002; Henke 2007a, b, 2010a). Scientific explanation, as opposed to mere narration or "just so stories" and myths, has to invoke lawlike regularities connecting causes and effects and to aim to a concise hypothesis testing or at least *quasi*-hypothesis testing (see Vogel 1975; Foley 1987; Henke and Rothe 1994, 1999a, 2005).

Studies on the evolution of social-behavioral systems, kin selection, intersexual and intrasexual selection, cognitive abilities, tool using and tool making, Machiavellian strategies, competition, coalitions, and alliances, which is the total complexity of social systems in primates, especially in apes, have become essential for paleoanthropological modeling (Foley 1987, 1995a, b; Tattersall 1998, 2011; Eckardt 2000; Henke and Rothe 2003; Henke 2003a, 2008; Rothe and Henke 2005; Henke and Herrgen 2012). Besides primatological field studies, which have given us a totally new view on the cultural capabilities of nonhuman primates (Goodall 1986), there is much to learn about our brains and the development of language and our emotions from all kinds of laboratory research [e.g., molecular biology (O'Rourke et al. 2000; Relethford 2001; Enard 2005), psychobiology

(Cartmill 1990a, b; Mithen 1996; Tomasello 1999; Withen 2000; Call and Tomasello 2008; Sommer 2007a, b; Sterelny 2012; Henke and Herrgen 2012)]. There is challenging news from the paleogenetic labs: Various genes are implicated in specifically human capabilities, e.g., language capabilities as indicated by FOXP2 (Enard et al. 2002; Enard 2005); autism (Green et al. 2010a, b); mental capacities (by Human accelerated regions – HAR; on abnormal spindle-like microcephaly-associated protein, ASPM (Pollard et al. 2006; Pollard 2009); on myosin heavy chain 16 (MYH16) which is associated with masticatory structures (Stedman et al. 2005; overview in Jobling et al. (2004). Varki and Altheide (2005) are "Comparing the human and chimpanzee genomes: Searching for needles in a haystack." I'm sure they will find many and inspire the field of human evolution tremendously.

It seems – to say it cautiously – that ancient DNA findings have recently solved one of the "oldest questions" in paleoanthropology that remained unsolved for more than 150 years. After the excavation of the name-giving fossils from the Neander Valley, near Düsseldorf in Germany, the "role of the Neanderthals" is subject to intense discussion (Spencer 1984; Stringer and Gamble 1993; Henke and Rothe 1994, 1999b; Tattersall 1995; Krings et al. 1997; Wolpoff 1999; Relethford 2001; Finlayson 2004; Harvati and Harrison 2006). As has been shown above, also heavily debated are the "Out of Africa" models, with and without hybridization: the *Assimilation model* and the *Multiregional model*. After never-ending and often contradictory discussions on molecular biological results assuming a total replacement of all archaic non-African populations by anatomical-modern *Homo sapiens* dispersing from Africa (see, e.g., Henke 2005; Relethford 2009; Cartmill and Smith 2009), and after many supposedly "infallible" statements that there was no hybridization of Neanderthals and modern humans (e.g., *cell* cover: "Neanderthals Are not Our Ancestors" (Krings et al. 1997), now – what a surprise – the message is that "Neanderthals bred with modern humans" (Green et al. 2010a, b). Paleogeneticists from Harvard and the MPI EVA, Leipzig wrote: "Comparisons of DNA sequences between Neanderthals and present-day humans have shown that Neandertals share more genetic variants with non-Africans than with Africans. This could be due to interbreeding between Neandertals and modern humans when the two groups met subsequent to the emergence of modern humans outside Africa. However, it could also be due to population structure that antedates the origin of Neandertal ancestors in Africa" (Sankararaman et al. 2012, abstract). Here is apparent strong support for the recent interbreeding hypothesis. Will this be the end of discussion? Time will tell!

Behavioral Modernity: What Pushed Us into Another League?

As shown above, the conceptual transition toward the "New Physical Anthropology" sensu Washburn (1951) and the steady optimization and increase of methodological approaches and technical skills during the last 60 years have succeeded in explaining us as "*another unique species*," to repeat Foley's paradox (Howell 2003;

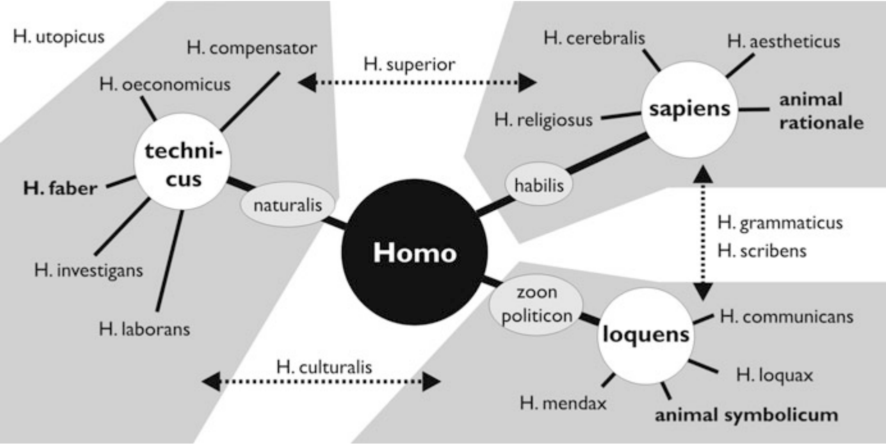


Fig. 12 Conceptions of modern humans as animals which have culture as an evolved constitutional – *tradi*genetical – component (Designed by Herrgen 2008; adapted from Henke and Herrgen 2012)

Fuentes 2010; Larsen 2010; Stini 2010). Paleoanthropologists and their colleagues from neighboring disciplines succeeded in explaining in biological terms the specific morphological and physiological features that set us apart from other primates, e.g., upright bipedal walking, orthognathy, extensive neencephalization, reproductive physiology and biology, loss of body hair, and a wide set of further traits, including skin colors; the latter is insofar important as it breaks racial prejudice (see Jablonski 2012).

Paleobiologists have solved the questions of when, where, and how these specific human patterns evolved, and sometimes "why" too. The most contentious answers are those on causes and consequences; in other words, we have a broad knowledge (or rather think we do) of the selective advantages of the human adaptive morphophysiological pattern. Tattersall (2006, p. 155) stressed wisely, "that the acquisition of novelties cannot be driven by natural selection, which can only favor new structures after the fact," and explains subsequently: "…that any novelty has to rise initially as an exaptation [synonym for preadaptation, add. W.H.], a structure existing independently of any new function for which it might later be co-opted."

Paleoanthropologists have reached wide consensus on the long-term channeling of pathways in primate evolution. They have built up plausible scenarios on the evolution of uprightness and bipedal walking, on the formation of a gracile masticatory apparatus, and on the excessive increase of cranial capacities. So far so good; but evolutionary anthropologists also have to explain our special behavioral pattern (see Fig. 12). They have to elucidate how our specific human information and social systems arose, how humans reached their unique cognitive abilities for name-giving thinking processes, for verbal speech, for extremely complex social traditions, for an extremely complex Machiavellian intelligence, and for the capability of environmental buffering (overviews in Vogel 1975; Withen 2000; de Waal 2001; Rothe and Henke 2005; Gädenfors 2003; Mithen 2005; Tattersall 2006, 2011; Henke 2007a, b, 2008; Klein 2009; Henke and Herrgen 2012; Sterelny 2012; Henke 2015 in print).

The challenge is also to explain the *total pattern* – human biology *and* culture (or better all cultural abilities!) – and to decipher the evolutionary factors and environmental influences that triggered the transitional process. After decades of very successful deciphering of the evolutionary trends within the order of Primates that led to the evolution of our genus *Homo*, we are – after a long "approach-run" – currently faced with the fundamental challenge to reconstruct the evolution of behavioral modernity, sometimes called "humanization," as the last step of the process of "hominization"; both terms sound like a teleological program, what they aren't; evolution has no goal!

During the last decades, there has been done much innovative inter- and multidisciplinary research to get the right answers to ancient anthropological questions: How could an evolutionary process bring about a culturally dependent primate or animal rationale (sensu Artistotle) *rsp*. animal symbolicum (sensu Cassirer 1923–1929)? (See Herrgen 2008; Henke and Herrgen 2012; Henke 2015 in print.) It is becoming significantly evident from primatological research that neither tool using nor tool making, nor hunting, nor food sharing, nor social intelligence and coalitions, nor Machiavellian intelligence, is a unique feature of *Homo sapiens*. So human biologists, cognitive psychologists, and primatologists had to look for other traits which set us apart.

The crucial question is: What pushed us into another league? The explanation has to come by "Darwinian" thinking (Sommer 2007a, b), as evolutionary anthropologists become increasingly critical about those caged in cultural prejudices.

The uniquely human behavioral pattern which made our species so successful, which we call behavioral modernity, is commonly explained as a change in the intrinsic cognitive competence of modern humans. It is described in terms of new capacities for cognitive breakthroughs, like evolution and/or perfection of language, meaning creation (synonyms are theory of mind or mind reading), and symbol use (symbolicity or symbolic thoughts). Kim Sterelny's definition of behavioral modernity is the following: "humans became behaviourally modern when they could reliably transmit accumulated informational capital to the next generation, and transmit it with sufficient precision for innovations to be preserved and accumulated" (Sterelny 2011, p. 809; see also Sterelny 2012; Henke 2015 in print). The last step of becoming human and even *humane*, i.e., an animal with the ability to empathize, to understand the intentions of others, to plan and to deceive, and to use symbols and language, is a recent topic of research. Three abilities of modern human behavior have come under special scrutiny: *language*, *theory of mind*, and *symbolism* (for a more complex approach, see, e.g., Cartmill 1990a, b; Noble and Davidson 1996; Mithen 1996, 1998, 2005; Tattersall 1998, 2002, 2006, 2012; Tomasello 1999; Withen 2000; Crow 2002; Gärdenfors 2003; Henshilwood et al. 2004, 2009; Wuketits and Antweiler 2004; Haidle 2006; Balter 2008;

Cartmill and Smith 2009; Conard 2009, 2010; Klein 2009; Henshilwood and d'Errico 2011; Henke 2015 in print). Cartmill and Smith (2009, p. 416) state: "it seems reasonable to think that language preceded the onset of art, religion, and other sorts of symbolic behavior in the course of human evolution." But how do we know this is fact? Research on paleogenetic features as FOXP2, morphological studies on hyoid bones, and cranial endocasts currently give little hope of proving this. No doubt, we are on very difficult terrain here.

And as regards mind reading and symbolism, there has been much progress from artifacts, mentifacts, and sociofacts (see Posner 1993; Renfrew and Zubrow 1994; Holzmüller 1997; Renfrew 1998; Mithen 1998; Marean and Thompson 2003; Wuketits and Antweiler 2004; Bar-Yosef and Zilhão 2006; Kappeler and Silk 2009; Klein 2009; Conard 2010; Nowell 2010; Sousa and Counha 2012; Sterelny 2012). However, detractors ask how we can reconstruct arbitrary, socially constructed conventions of our ancient Pleistocene antecedents, if understanding of symbols is often restricted to persons sharing a common cultural background, i.e., the same "cognitive map"? Bredholt-Christensen and Warburton (2003, p. 40) caution, referring to the insider/outsider debate, that we run the following risk: "In attempting to understand the people under study we create categories by which we distinguish phenomena of their culture. On this basis (prehistoric "symbols" being "our" interpretation of "*their*" world as "*we*" see it)." The authors emphasize that this doesn't mean that posing questions about prehistoric symbolism and archaeological differentiations are irrelevant and illegitimate; however, such queries can only be answered on an *etic*, not on an *emic* level (Bredholt-Christensen and Warburton 2003, p. 39; for more discussion on more "*Criteria of Symbolicity*," see positions papers of the 9th Annual Meeting of the EAA, 2003; Bouissac 2003). When discussing "how *Homo* became *sapiens*" (see Gärdenfors 2003, book title) and how our ancestor developed full modern behavioral modernity, we are faced with a major problem of anthropology (Marean and Thompson 2003). By an integrated multidisciplinary approach, including paleoanthropology, archaeology, primate ethology, ethnology, cognitive psychology, and evolutionary genetics, we can hope to find answers to the most intriguing question: How could the self-organizing process of hominization bring about a culturally dependent organism that has "*culture as its nature*" (sensu Vogel 2000)?. From a sociobiological perspective, we have to talk about "culture *via* nature" as there are convincing arguments "that culture has been so successful biologically because it gives humans improved possibilities for coping with the perils of life and so increases the chance of survival. [...] Whatever defines culture, it is based on adaptive imitation, or "imitation of the fittest"" (see Voland 2000b, p. 196).

To perform the imperative "*Nosce te ipsum*!" we need a concentrated and concerted approach by all evolutionary biological and cultural sciences, taking a strictly "Darwinian perspective" and with special focus on the "human niche" of *Homo sapiens*. We have to know much more about the totality of the special conditions of early anatomical-modern *Homo sapiens* hunter-gatherers that made their lives – and survival – possible; otherwise, we will never understand the "constitutional preadaptation" affecting the final step to "behavioral modernity" and our specific "design" which evolved *without* a "designer." To prove this Darwinian message is more than enough motivation for future research on the origin of the human mind.

Conclusion

Don't Expect Too Much: We Are Just Modeling!

When we sum up the history of paleoanthropological research, it becomes evident that the paradigmatic change initiated by Darwin's realization of a true historical genetic kinship of all living organisms stimulated enormous interest in questions of human origins. Those research subjects that promised to solve the enigma of anthropogenesis in Darwin's days were the natural sciences (paleontology, geology, comparative anatomy *rsp*. morphology, zoology, and human biology), on the one hand, and the social sciences of prehistory and ethnology, on the other.

The "conglomerate" of natural sciences contributed to a pretty slow formation of "human paleontology" *rsp*. "paleoanthropology" and was joined at its very beginning by the social sciences. However, the segregation of the diverse disciplines in the natural, medical, and social faculties hampered an integrative approach, even apart from the skepticism toward, and even rejection of, Darwinian evolutionary theory by a great part of the scientific community. Rudolf Virchow was by far no exception.

In retrospect, it is apparent that paleoanthropology long failed to adopt a Darwinian evolutionary approach. Its methodology remained – with some commendable exceptions – mainly casuistic, descriptive, and nonanalytical. This didn't even change at the beginning of the twentieth century, when classical genetics began after the rediscovery of the Mendelian laws. Notably, even after the formation of the "Modern Synthesis," (paleo)anthropology perpetuated long-standing erroneous conceptions (i.e., polygenism, orthogenism, Eurocentrism, ethnocentrism, social Darwinism, racism). It can be concluded that paleoanthropology remained "simple minded" until after World War II, without conceptual integration of Darwinian and Neo-Darwinian concepts. However, subsequently, evolutionary biology has become the fundamental superstructure, as already explicitly formulated by the population geneticist Theodosius Dobzhansky (1937) and his outstanding colleagues from other biological sciences.

As a recognizable, valid subject of evolutionary biological science, paleoanthropology was established for the first time in the early 1950s by Sherwood L. Washburn (1951, 1953). The conceptualization and foundation of paleoanthropology/paleobiology as a subdiscipline of the "New Physical Anthropology" was correlated with the adoption of the concepts of Darwinian theory and those of the "Modern Synthesis." This was followed by a period of severe problems in the recognition of taxic diversification and speciation processes when paleoanthropological findings increased exponentially and the fossil record and the "Modern Synthesis" came under critical observation (Eldredge and Gould 1972;

Tattersall 1998, 2000a, b; Foley 2001; see also Wolpoff 1996–1997). Once again, paleoanthropology had a slow start compared to other evolutionary sciences. However, due to crucial conceptual support by outstanding scientists, e.g., Sherwood L. Washburn, F. Clark Howell, Louis S. B. Leakey, Phillip V. Tobias, and many other enthusiastic colleagues, the field was revivified by new fossils and essential findings from field and laboratory research.

Paleoanthropology has now evolved to become a complex research strategy of evolutionary biology that integrates all facets of comparative functional and evolutionary anatomy, primatology, behavioral ecology, cognitive primatology and sociobiology, molecular and population genetics, paleogenetics, as well as earth sciences, archaeology, archaeometry, and ethnology. Since the 1960s and 1970s, there has been developed a large body of empirical knowledge related to international collaborative networks, all underpinned by epistemological discourse. The enhanced armamentarium of perspectives and methodologies was drawn largely from the diverse natural sciences and from conceptual progress in archaeology and ethnology too. Paleoanthropology benefited from the high innovativeness of the natural and associated social sciences and from the increasing complexity of its approaches, as well as from exceptional fossils, surprising findings, and a vast public interest due to new media.

Embedded in evolutionary biology, and adjacent to a broadly based scientific field with theory-guided empirical approaches, paleoanthropology has finally since the 1970s become a mature science. The consistent integration into the wider set of biological sciences underpinned by the revised System Theory of Evolution provides a road map for a successful research design in paleoanthropology. Students should follow this program to achieve reliable and valid findings and to build up reasonable scenarios of the past. However, one should have Robert Foley's four "pathways to the past" always in mind: "Neither theory nor models on their own are sufficient in palaeoanthropology, for they would amount to composing the present on the past. [. . .] Just as the fossils are mute without the frame work of theory, so, too, the theory is self-confirming when not put to empirical tests." He suggests testing the strength of "inferences," using "isolating techniques," and applying "probabilistic" and "comparative biological" tests. Though this seems to be "the appropriate framework for investigating patterns in hominid evolution" (see Foley 1987, p. 90), it's necessary to emphasize that the complexity of human origins can only be understood correctly if we are always aware of our potential prejudices.

Always Being Aware of Biases and Misunderstandings

Paleoanthropologists should always be aware of the principal aims of scientific work (Mahner and Bunge 2000). This allows them to avoid the pitfalls of naïve storytelling and of obscuring their aims with narrative. In spite of the paradigmatic change to a teleonomic explanation of life, there is plenty of evidence that even though "scientific thought is subject not only to the force of empirical knowledge, there doubtlessly is under changing conditions much impact from social constraints" (Stoczkowski 2002, p. 1; Henke 2010a; Sarasin and Sommer 2010). In his "Explaining Human Origins – Myth, Imagination and Conjuncture," the prehistorian and archaeologist Wiktor Stoczkowski (2002) presents a table of distinctive characteristics of humans in general and of primitive humanity in particular, as described in our sample of hominization scenarios. The characteristics most often mentioned as triggering human evolution are ranked by their assumed importance: tools, bipedalism, free hands, language, social life, voluminous brain, superior mental faculties, reduced canines, cooperation, sexual division of labor, food sharing, hunting, perfectibility, family organization, productive success, prolonged childhood, absence of estrus, and carnivorous diet.

Even when neglecting obviously outdated "traditionalist" and "Lamarckian" approaches to explain anthropogenesis in Darwinian terms, Stoczkowski (2002, p. 198) states that "contrary to what is often thought, scientists do not draw their conclusion from empirical data, any more than they rewrite history in terms of prevailing ideology." Since the French original of this work, *Anthropologie naïve, anthropologie savante* was published 20 years ago, in 1994, I am convinced that in saying this, the author has remained in ignorance of much of the theoretical and analytical progress made by current paleoanthropology. Stoczkowski clearly had not considered the more recent phase of "empirical tests" in modeling the past, although it is true that earlier human origin models were one sided and monocausal and missed the required complexity.

This applies, for instance, to the "Man the Hunter" model of Lee and DeVore (1968), the "Food sharing behavior" model of Isaac (1978), the "Hunter-Gatherer" model of Zihlman and Tanner (1978), the "Pair bonding" model of Lovejoy (1981), the "Nutrition strategy" model of Hill (1982), and the "Scavenging" model of Blumenschine and Cavallo (1992). This is not the place to discuss the validity of analogue and concept models or the theoretical patterns of recognition techniques and the appropriateness of optimality principles (overviews in Foley 1987, 1995a, b; Henke and Rothe 1994); but it should be noted that more recent models of human origins, e.g., Aiello and Wheeler's (1995) "Expensive tissue hypothesis," O'Connell et al.'s (1999) "Grandmothering hypothesis," and Wrangham et al.'s (1999) "The Raw and the Stolen; Cooking and the Ecology of Human Origins" model take into account the complexity of the network of causes for social transitions. Further, paying attention to life history, energetic and ecological components of the ecological niche concept have caused much improvement and progress (overviews in Henke 2007a, 2010c; Henke and Herrgen 2012; Kaplan et al. 2000). Foley and Gamble (2009, p. 3267) are aware that "the evolution of 'human society' is underpinned by ecological factors, but these are influenced as much by technological and behavioural innovations as external environmental change."

However, our answers to the why-questions are still contentious and possibly will remain that way. Additionally, what has previously remained unmentioned is that some hominization models were severely flawed by the fact that anthropology was until recently a male-dominated science. The comparison of the prevailing male perspectives with views by feminist researchers demonstrates that paleoanthropology, prehistory, and sociobiology were in particular influenced by androcentrism. Adrienne Zihlman and Nancy Makepeace Tanner were the first (in the 1970s) to complain about androcentric misinterpretations of the female role in human evolutionary history. Their critique of the "Man the Hunter" scenario was a groundbreaking event for feminist anthropology (e.g., Tanner and Zihlman 1976; Zihlman 1978, 1981; Linda Fedigan 1986, 1992; Margaret Ehrenberg 1989; Inge Schröder 1994; Melanie Wiber 1997; Lori Hager 1997; Londa Schiebinger 1999; James M Adavasio et al. 1999; see also Henke et al. 1996; Henke 1997). Linda Fedigan (1992, p. 306) put it this way: "The assumption that females are losers in competition between the sexes, although widespread in sociobiological literature, does not seem to me inherently necessary to evolutionary theories, precisely because it is a cultural assumption rather than a biological given."

In this context, one should also ask: Are there still other biased perspectives that require a closer review by science history? This is quite likely, as some good research work has already been done on the presentation of "lost worlds" and paleoanthropological ideas in print media and movies, as well as in scientific art, popular scientific illustrations, and museum exhibitions (see, e.g., Ickerodt 2005; Kleeberg et al. 2005; Hurel 2006; Crawford 2007; Sommer 2008; Sommer et al. 2008; Goodall 2009; Kort and Hollein 2009; Sarasin and Sommer 2010; Ingensiep 2013).

Furthermore, while it is well known that Christian doctrine and other religious beliefs have demonstrably influenced research on and discussion of human origins in the past, the impact of social and political ideologies on paleoanthropology is a largely unexplored field that offers great possibilities for future historical research. There is, especially, a need to study the impact of sociocentrism, ethnocentrism, and nationalism on interpretations of human origins, as well as national and regional museological conceptions (see, e.g., Schmalzer 2008, Africa; Vickery 2013; Durband (2009) Southeast Asia and Australia; Durband 2009, excellent overviews to the issue in Sarasin and Sommer 2010).

A further issue of historical interest is the relationships of colonialism and paleoanthropology; Goodrum (2009, p. 349) remarks that: "The implications of European and American researchers conducting excavations and removing hominid fossils from Asian and African countries during and following the colonial period is another subject that remains largely unexplored."

And one can bring the same question to recent times: How has the experience of outstanding foreign students trained at American and European universities translated back to their native countries and their subsequent research? Did they bring back new perspectives, and have their researches specially influenced paleoanthropology and their own societies? (See, e.g., Sperber 1990; Lille and Kennedy 2010)

Knowledge Commits to Responsibility!

Besides the diverse "**-***ism*" issues mentioned above, there is a vast "construction site" in paleoanthropology based on transmitting facts – and not fiction – about human evolution to the general public. Paleoanthropologists benefit from enormous public interest in their field; but big problems can arise if the preconceptions of that public are wrong or if their understanding is merely superficial. Transmitting scientific findings to the public is not an easy task and demands great precision; the difficulties involved are proven by the daily experience of lecturers and teachers. Empirical-didactical research by Graf and Soran (2010) provided disillusioning results: Evolution as pattern and process is even today very poorly understood and misinterpreted by the broad public, even though the basic theoretical framework is biologically undisputed. There is a reluctance to understand that there are still unsolved problems out there; science is a process (see Toepfer 2011; Wrede and Wrede 2013). Of greatest relevance is that there is widespread misunderstanding of evolution itself [e.g., that "evolution" aims the preservation of species; evolutionary adaptations are adaptations to recent environments; organisms are perfectly adapted; humans are the crown of evolution; evolution is a simultaneous progress and has an aim; nature is harmony; and nature is "good" and has morality (overview in Henke and Herrgen 2012)]. All this is of relevance for paleoanthropology, since one of the main general insights from the Darwinian paradigm is that we, as modern humans, have to take responsibility ("Das Prinzip Verantwortung," formulated by Hans Jonas; see Altner 1981a), because we are the single organism on earth with morality (Vogel 2000; Cela-Conde and Ayala 2004; Bischof 2012). Washburn (1968, cit. by Fuentes 2010, p. 5) wrote that "human biology has no meaning without society [. . .] the evolution of man can only be understood as a biosocial problem." A proper understanding of evolution is thus essential for modern societies; and when taking responsibility is a social concern, it is clearly necessary to publish scientific results on human evolution not only in scientific journals but also in the public media. Still, while sophisticated popular scientific writing is highly welcome and helpful (see call by Howell 2003; Fuentes 2010, p. 5), superficial and callow fossil – and journalism-driven science initiated by pure sensationalism – is counterproductive. What we need to do in our popular nonfiction is, as Howells (2003, cit. in Fuentes 2010, p. 5) urged, to "adopt modern perspectives of an emergent evolutionary biology, and practice analytical, comparative, and experimental methods, relevant to elucidation of the nature and roots of the Human condition." Howells injunction remains the standard, and fortunately there are currently excellent popular expositions in the bookstores, e.g., Tattersall's (2012) *The Masters of the Planet* and Stringer C (2013) *Origin of our Species*.

Yes, Science History Matters!

With the methodological principles of the biological and neighboring sciences in mind, paleoanthropologists should also be aware of science history. In the words of Theunissen (2001, p. 147): "That 'history matters' is perfectly obvious if it is taken to mean that the present cannot be understood without reference to the past." Although this statement might seem trivial, there is a dilemma, mentioned by Foley (1987); the past is a "foreign country" and our forerunners did things differently there. The challenge of paleoanthropology is to improve our scientific methodology, to learn more about us and our origin, in order to reach a biological and sociobiological self-conception (Vogel 2000). The historicist approach may give rise to reflexive doubt, so don't expect too much. Dennell (2001, p. 64) is regrettably right when saying: "Whilst we might like to think that palaeoanthropology is a discipline that unifies humanity and helps combat racial, sexist, and other types of prejudice simply because of its focus on the origins of humankind, we should not forget it did the opposite for at least the first half of the twentieth century."

The confidence of being on the right road raises the risk of complacency. And therein lies the essential reason why history really matters; one should never be too comfortable for too long with an idea (Dennell 2001). What is needed is a real and intense dialogue between the many disciplines that cooperate to unravel the process of human origin. The history of paleoanthropology teaches us, in all its facets and complex details, quite how great a challenge of evolutionary biology reconstructing our origin is. McHenry (1996, p. 86) has put it neatly: "One needs to make the best of our tiny sample of life in the past, to be open to new discoveries and ideas, and to enjoy the pleasure of learning and changing." No one will explain our human origins, if we don't – and what a fascinating challenge!

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Modeling the Past: Archaeology
- ▶ Modeling the Past: The Primatological Approach
- ▶ Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Patterns of Diversification and Extinction
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of Speech and Language
- ▶ The Evolution of the Hominid Brain
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ Virtual Anthropology and Biomechanics

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Charles Darwin, Paleoanthropology, and the Modern Synthesis

Franz M. Wuketits

Contents

Abstract

The present chapter focuses the role that paleoanthropology played in Charles Darwin's views of evolution and in the formation of the synthetic theory or modern synthesis. It shows the close relationship between these evolutionary conceptions and the central goals of paleontology. Darwin was among the few naturalists in the nineteenth century who fully grasped the importance of fossils for an understanding of evolution. In spite of the incompleteness of the fossil record – and despite opposing views – he referred to paleontology in order to support his theories of common descent and continuous steps in evolutionary history (gradualism) as well as his views on the roots of humans in apelike

F.M. Wuketits (✉)
Institut für Philosophie, Universität Wien, Wien, Austria
e-mail: franz.wuketits@univie.ac.at

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mammals. Thus, in his *The Descent of Man* he argued, with some optimism, that the lack of fossil human remains was merely due to the fact that they had not yet been discovered. Indeed, paleoanthropology as a discipline at the interface between paleontology and anthropology was firmly established only in the late nineteenth century. However, up to now it has played a major part in the study of human evolution, and it has also helped in establishing the synthetic theory in the 1940s and 1950s, although only few of the leading proponents of this theory were explicitly concerned with paleoanthropological issues. The synthetic theory has been extraordinary successful as a comprehensive explanation of the mechanisms of evolutionary change of species (mainly variation and natural selection), and it has offered convincing evidence that the very same mechanisms fully apply to human evolution. This chapter also includes some (historical) examples which show how paleoanthropologists were sometimes misguided by ideological questions (*Weltanschauungsfragen*). Moreover, it brings into the focus some methodological issues and the shift of paleoanthropology from mere narrative to a theory-guided science. These issues are serious, since after all they affect the status of a discipline that is of crucial importance for a deep understanding of past and present conditions of humankind. Finally, therefore, the chapter considers the importance of paleoanthropology as the basis for a synthesis of anthropology that is increasingly needed as the latter gets more and more split into a growing number of highly specialized subdisciplines.

Introduction

"Paleoanthropology tries to establish a valid phylogenetic model on the adaptive processes that made us human. As a result of sophisticated planned excavations there has actually been a dramatic increase in fossilized bones and archaeological material, which enables us to unravel our history and its spatial and chronological patterns" (Henke 2005, p. 120). However, there is agreement that fossil and archaeological material is not enough, because any remain of the past requires a theoretical interpretation. The frame for such an interpretation is the theory of evolution. Without this theory, fossils give much room for wild speculations, as can be seen from the role they played – or even still play – in mythology and folklore beliefs (see Thenius and Vavra 1996). The very aim of paleontology is the reconstruction of the history of life on earth (Kuhn-Schnyder and Rieber 1984), and this clearly presupposes that, first, life has a history and, second, that the extant species descended from earlier ones. Hence, paleontology and the theory of evolution are strongly connected with each other.

Evolution is studied in many disciplines and by the means of different tools. Paleontology is one of them, but it is the only field of research that – as a historical science at the intersection between geology and biology (Hölder 1985; Thenius 1972) – offers a direct access to life of the past. "The fossil record provides a powerful basis for analyzing the controlling factors and impact of biological evolution over a wide range of temporal and spatial scales and in the context of an evolving Earth" (Jablonski 1999, p. 2114).

The discovery of a calotte and postcranial skeleton in Neanderthal near Düsseldorf (Germany) in 1856 – 3 years before Darwin's publication of *On the Origin of Species* – was the beginning of paleoanthropology. The Neanderthal man, however, gave rise to many speculations and controversial interpretations, and it took some time to put this discovery – together with other findings documenting the existence of this fossil human species – in the right place. Anyway, soon – and perhaps inevitably – the Neanderthal man was brought into connection with evolution, and it was, hesitantly, concluded that he could be an ancestor of modern humans (Tattersall 1995). Many controversial discussions concerning the evolutionary status of humans followed, and still there are "open" questions regarding the history of the hominin branch. Yet the close connection between paleoanthropological research and findings and conceptions in many other disciplines (recently including molecular biology) gives us today a quite comprehensive understanding of the processes of hominization. The theories underlying this understanding have been Darwin's theory, the synthetic theory and finally an organismic, systemic approach to evolution. The – rather short – history of evolutionary thinking in general can be seen as a process towards an extension of evolutionary theory. Ever since Darwin evolutionary theories have covered more and more empirical data and assembled them to a coherent system of knowledge. Dobzhansky's well-known and frequently cited statement – "Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973) – has proved to be entirely right.

In what follows, first a brief historical sketch of evolutionary thinking with special reference to Darwin is given. Second, some reflections on the status of paleoanthropology are presented. Third, the formation and implications of the synthetic theory are outlined. Forth and finally, the need of synthesis in anthropology is expressed.

Charles Darwin's Conceptions of Evolution

Darwin and the Emergence of Evolutionary Thinking

The publication of Darwin's monumental *On the Origin of Species* was the climax of a long intellectual development (see, e.g., Bowler 1984; Eiseley 1961; Glass et al. 1959; Junker and Hoßfeld 2001; Oeser 1996; Zimmermann 1953). At the beginning of this development, we find quite cautiously pronounced ideas about the variability of species, speculations concerning a changeable universe, and the place of humans in it. For example, Denis Diderot (1713–1784), one of the chief proponents of the French Enlightenment, stated that "if beings change successively, passing through the most imperceptible nuances, time, which does not stop, must eventually put the greatest difference between forms that existed in ancient times, those which exist today and those that will exist in far-off centuries" (quoted after Crocker 1959, p. 129). And Diderot's compatriot and contemporary, the eminent and celebrated naturalist Georges L. L. Buffon (1707–1788), reasoned as follows: “Though Nature appears always the same, she passes nevertheless through a constant movement of successive variations . . .; she lends herself to new combinations, to mutations of matter and form, so that today she is quite different from what she was at the beginning or even at later periods” (quoted after Lovejoy 1959, p. 104).

Diderot, Buffon, and some other scholars – naturalists and philosophers – of the eighteenth century marked one of the most exciting and momentous transformations in the history of Western thinking: the shift from a static to a dynamic conception of nature. However, they had to meet serious obstacles. For many centuries the only accepted source for an “explanation” of the existence of all things, living and nonliving, was the Old Testament, and it was taken for granted that the Creation story of Genesis reveals the ultimate and unquestionable truth about the origin of the earth and its inhabitants. It was considered as a matter of course that humans are the creation of a benevolent God who had created them in his own image. Natural theology was the most influential and pervasive doctrine in the eighteenth and even in the nineteenth century. Natural theologians, among them – and above all – William Paley (1743–1805), argued that the organization of living beings offered evidence for an omnipotent and omniscient designer and did not leave any space for alternative ideas. Hence, it should not come as a surprise that even when evolutionary thinking in the nineteenth century became more or less popular, many scholars did not abandon theological interpretations of nature and tried to combine evolution with transcendentalism and spiritualism.

The static conception of the world is strongly connected with typological thinking or essentialism (Popper 1960) which is deeply rooted in Western philosophy and still quite influential. In the eyes of a “typologist,” only “ideas” or “essences” are real, while any observed object is just their manifestation; ideas or essences are unchangeable, and they give the observable natural objects their “fixed” character. In a static world the notion of time does not play a significant role, and as long as people believed that the earth and all living beings were created at once some 6,000 years ago, they could neither grasp the variability of species nor the species’ common descent. Some naturalists in the eighteenth century – particularly Buffon – did speculate that the earth could be many thousand or even million years old, but geological time and history were not truly realized before the nineteenth century (Gould 1988).

Anyway, speculations about the possibility of long-term changes in nature and the possible variability of plant and animal species through longer periods of time do not necessarily imply – or lead to – an evolutionary theory in a strict sense. Such a theory has to pose and to answer at least three sets of questions (Wuketits 1988, 2005b):

- Are species changeable? Are the extant species descendants of other, earlier species?
- What are the modes and pathways of evolution? Does evolution occur step by step, by slow gradation, or does it allow discontinuities? To what degree are

species and "categories" of organisms (such as families, orders, or classes) related to each other?
- What are the mechanisms, the "motors" of evolutionary change?

The first question marked the very beginning of evolutionary thinking and is no longer relevant because evolution has turned out to be simply a fact. However, the statement that species are indeed changeable does not yet imply a theory of evolutionary changes and is not a theory by itself. It was common to speak in this context of a "theory," as long as "there was some likelihood that it was incorrect and that evolutionary descent had not occurred" (Ayala and Valentine 1979, p. 1). Any theory of evolution has to answer the second and the third set of questions.

In this strict sense the French naturalist Jean B. de Lamarck (1744–1829) was the first evolutionary theorist (see, e.g., Junker and Hoßfeld 2001; Oeser 1996; Wuketits 1988, 2005b, 2009b). Lamarck was a prolific researcher and contributed to a wide spectrum of scientific disciplines. He did not just speculate about the possibility of evolution, but explicitly stated that complex organisms had evolved from simpler ones. Also, he tried to find out the branching of animal groups and – most important – to specify mechanisms of evolutionary change. In first instance he is – rightly or wrongly – remembered as an advocate of the idea of the "inheritance of acquired characteristics" that is commonly known as Lamarckism.

It is a remarkable historical coincidence that Lamarck published his main methodological work, his *Philosophie zoologique* (*Zoological philosophy*), in Darwin's year of birth and 50 years before the publication of Darwin's *On the Origin of Species*. Although Lamarck did attract the attention of scientists, philosophers, and political commentators throughout the nineteenth and twentieth centuries (Corsi 2011), it was not his but Darwin's work which gave the theory of evolution its final impetus and brought it into the focus of public interest. "No biologist," says Mayr (2000, p. 80), "has been responsible for more – and for more drastic – modifications of the average person's worldview than Charles Darwin." One may doubt that any "average person" in his or her everyday life really bothers about Darwin, but everybody who takes Darwin seriously can no longer adhere to the traditional static worldview (chapter "▶ Evolution of Religion," Vol. 3).

At the beginning of his scientific career, Charles Darwin (1809–1882) believed in creation and was not aware of Lamarck and other scholars who at least tentatively had approached the idea of evolution. He studied theology, learned Paley's doctrine of natural theology by heart, and was prepared for Holy Orders in the Church of England. His *Beagle* voyage (1831–1836) (see Darwin Keynes 1988), however, which gave him many opportunities to observe biological and geological phenomena and to collect a vast number of biological and geological objects, led to dramatic changes in his intellectual life. Sure, already as a theology student (and even earlier), Darwin had been very much fascinated by such objects and attended courses and excursions in botany, zoology, and geology, but since at that time many, if not most, naturalists were Christians or even clergymen, he could not see any contrast between science and the Christian dogma. Besides, he never studied – according to our today's standards – natural sciences at a professional level and represented, in a way, the typical amateur naturalist in nineteenth-century England (Finkelstein 2000).

When Darwin, after his *Beagle* voyage, returned to England, not only his prospects of a parochial life had vanished but his belief in the variability of species had developed. For the next two decades, he was busy studying the collected material and formulating his views of the transmutation of organisms (see, e.g., Ospovat 1981). According to his character – he did not care to hurry either in his private nor in his professional life – he proceeded very cautiously and long hesitated to publish his conclusions. “In June 1842,” he remembered in his *Autobiography* (edited more than 100 years later by his granddaughter Nora Barlow), “I allowed myself the satisfaction of writing a very brief abstract of my theory in pencil in 35 pages” (Darwin 1958, p. 120). But only 17 years later, he published his *On the Origin of Species* that became a landmark in the history of Western thinking. In the mean time, however, he published eight other books, among them a volume on the structure and distribution of coral reefs and – what particularly deserves to be mentioned – a comprehensive monograph in two volumes on a somewhat curious group of crustaceans, the Cirripedia (barnacles). This work can be regarded a “classic” in zoological literature. Thus, when Darwin released the *Origin* he was well established in the scientific community. Thomas H. Huxley (1825–1895), one of Darwin’s chief advocates (“Darwin’s bulldog”), remarked that Darwin “never did a wiser thing than when he devoted himself to the years of patience which the Cirripedia-book cost him” (Darwin 1888, p. 347). While he was thoroughly working on the anatomy and taxonomy of the barnacles for no less than 8 years, he already spent much time thinking about evolution, so that one may argue that this study of a special group of animals served him as a long-term empirical training for the sake of better argumentations in evolutionary thinking. And one can, as Ghiselin (1969) suggests, see connections between Darwin’s ideas on comparative anatomy applied to barnacles and his views of evolution.

Nora Barlow (1885–1989) writes in her introduction to Darwin’s *Autobiography* that “he had to convince himself by accumulated evidence before he could convince others, and his doubts are as freely expressed as his convictions. His books lie like stepping-stones to future knowledge” (Darwin 1958, p. 13). This is particularly true of his *On the Origin of Species*, which is probably best characterized as *One Long Argument* (Mayr 1991). In fact, Darwin intended to offer most convincing evidence for the variability of species and its major mechanism: natural selection (chapter “▶ Evolutionary Theory in Philosophical Focus,” Vol. 1). The *Origin* contains numerous data from different disciplines including geology, biogeography, anatomy, and embryology. Nevertheless, it would be wrong to believe that Darwin collected facts in order to, finally, establish a theory. Rather, his “scientific accomplishment must be attributed . . . to the development of theory” (Ghiselin 1969, p. 4). As he himself put it: “From my early youth I have had the strongest desire to understand or explain whatever I observed, – that is, to group all facts under some general laws” (Darwin 1958, p. 141).

The “law” of natural selection does give a substantial explanation of the variety of organisms, extant and extinct, and their changes through the ages. And it has had significant philosophical implications (chapters "▶ Evolutionary Theory in Philosophical Focus," Vol. 1, "▶ Evolution of Religion," Vol. 3, and "▶ Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology," Vol. 3), for it has made the "intelligent-design argument" obsolete. Darwin replaced the old and venerable concept of (universal) teleology by a very "profane" mechanism that operates on the basis of randomly produced individual varieties in each species and does not entail any plan or purpose in nature. Hence, he concluded that merely "from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows" (Darwin 1859 [1958], p. 450). The world into which Darwin led us is "a world in which man must rely on himself, in which he is not the darling of the gods but only another, albeit extraordinary aspect of nature" (Simpson 1963, p. 25). Early when he started to reflect on evolution, Darwin must have also human evolution in mind, but in the *Origin* he just – and somewhat cryptically – remarked that "much light will be thrown on the origin of man and his history" (Darwin 1859 [1958], p. 449).

Darwin's Theories and His Credit to the "Great Chain of Being"

However, in fact Darwin established five theories of evolution (Kutschera and Niklas 2004; Mayr 1991, 2000; Wuketits 2005a, b).

- Evolution as such: Species are not constant but variable.
- Common descent: All species are genealogically related and finally to be traced back to one single unique origin in the history of the earth.
- Multiplication of species: One species splits into two or more new species.
- Gradualism: Evolution occurs gradually, step by step, without major discontinuities.
- Natural selection: The very mechanism of evolution is natural selection; it acts on the ground of the abundance of genetic variation in each generation.

Here again a distinction must be made between the fact that species have changed through the ages and theories of the pathways of this change as well as its mechanisms (see also Ayala 2005). Darwin's work addressed all three issues. His well-informed and sympathetic contemporaries noticed that "the two great merits of this work are its bringing together in a condensed form the evidences in favor of the Evolution of Life, and its offering Natural Selection as a cause of this Evolution" (Chapman 1873, pp. 16–17). Since at the beginning of his reflections on the changeability of species Darwin was not aware of his "precursors" (including Lamarck), he discovered evolution once again and, as it were, for himself. Only later he paid tribute to scholars who had speculated on evolution before him and regarded Buffon as the first naturalist who had treated the variability of species in a serious scientific manner.

As is well known, Alfred Russel Wallace (1823–1913) had developed a theory of natural selection very similar to – or almost identical with – Darwin's theory. In June 1858 Darwin received a letter from Wallace and a manuscript in which he indeed found expressed his own ideas. Maybe that, as Ruse (1982, p. 3) speculates, Darwin's "heart started to sink," because for two decades he "had been sitting on a secret: a theory and a mechanism that would explain in a scientific way the organisms we find around us and in the fossil world." Anyway, he felt alarmed and informed his friends, among them Lyell (see section "Darwin and Paleoanthropology") about Wallace's text. Wallace's paper, then, was presented together with an excerpt of Darwin's nascent work at a meeting of the Linnean Society in July 1858, and Darwin felt pushed to complete and to publish his work as quickly as possible. However, what he finally released to the public, the *Origin*, was not what he actually had been preparing, a "big book" on evolution (Ospovat 1981). The "Darwin-Wallace story" still leaves space for speculations among evolutionists and historians of science as well. Here it should be sufficient to note that Wallace – who, by the way, was the founder of biogeography – must not be regarded as "a second Darwin" (Glaubrecht 2013). No matter that he had developed, independently of Darwin, a theory of natural selection (and coined the word "Darwinism" to characterize both, his own and Darwin's selection theory) – the two men disagreed with respect to some crucial implications of evolutionary thinking: Wallace embraced spiritism and was not prepared to fully apply the idea of evolution by natural selection to the emergence and evolutionary history of humans, while Darwin, though due to his personal dispositions, was not determined to become a revolutionary (Wuketits 1987) – revolutionized the Western world view and has been rightly considered one of the leading supporters of scientific materialism (chapters "▶ Historical Overview of Paleoanthropological Research," Vol. 1, "▶ Evolutionary Theory in Philosophical Focus," Vol. 1, and "▶ Evolution of Religion," Vol. 3).

This does not mean that Darwin broke with all traditions of Western thinking. As his views of gradualism show, he adhered to the long-lasting and venerable philosophical tradition, according to which there is continuity in nature: *natura non facit saltus*. Since ancient times the idea of a great chain of being (Lovejoy 1936) was – and to a certain extent still is – compelling. Up to the nineteenth century, scale-of-nature models (*scala naturae*) were very popular. They reflected the assumption that all natural objects – from inorganic compounds to objects of ever-higher complexity, plants and animals, and finally human beings – were arranged in a linear way. But these models were static and implied the conviction that the (linear) arrangement of natural objects represents the divine plan of creation. The natural objects followed, one after the other, but were not linked together by genealogy. Apparently, only the Swiss zoologist Charles Bonnet (1720–1793) approached the perspective that the scale of nature could produce some "branches" and thus, in a way, anticipated the model of a genealogical (phylogenetic) tree which, after all, was introduced by the German physician and zoologist Peter S. Pallas (1741–1811). Pallas replaced the idea of a mere succession in nature by the concept of a genealogical tree or a "net" by which he indicated that living beings are connected like nodes in a network (Oeser 1996; Zimmermann 1953). Hence, he came close to the theory of common descent which, then, in Darwin's work played a central role.

Clearly, in contrast to the scale-of-nature conceptions, Darwin advocated a dynamic and non-typological view of living beings and rejected the belief in a divine plan. His gradualism generally fits the idea of continuity in nature, but it cannot be separated from his theory of natural selection. Darwin (1859 [1958], p. 435) stated: "As natural selection acts solely by accumulating slight, successive, favourable variations, it can produce no great or sudden modifications; it can act only by short and slow steps. Hence, the canon of 'Natura non facit saltum', which every fresh addition to our knowledge tends to confirm, is on this theory intelligible." However, Darwin seriously considered the incompleteness of the fossil record and thus the missing of connecting links. "Why is not every geological formation charged with such links?," he asked, and "Why does not every collection of fossil remains afford plain evidence of the gradation and mutation of the forms of life?" (Darwin 1859 [1958], p. 429). Yet Darwin did not feel that his conceptions of evolution, here particularly gradualism, were weakened by the missing of fossils. Rather, he obviously believed that he had good reasons for some optimism, when he stated the following: "If we look to long enough intervals of time, geology plainly declares that species have all changed; and they have changed in the manner required by the theory, for they have changed slowly and in a graduated manner. We clearly see this in the fossil remains from consecutive formations invariably being much more closely related to each other, than are the fossils from widely separated formations" (Darwin 1859 [1958], p. 431).

It is important to notice that Darwin generally expected strong support for his views from geology and paleontology. This can be seen by the fact that in the *Origin*, he devoted two chapters to the geological and paleontological record. Also, it has to be mentioned that Darwin's notebooks – written in preparation for the "big book" – include material on paleontology and extinction (Ospovat 1981). All things considered, one has good reasons to state that paleontology played an important part not only in Darwin's gradualistic view of evolution but also in the formation of his other four theories. His theories should be seen as a coherent (theoretical) system. As soon as he started to believe that species are changeable, he also began to reflect on possible modes and mechanisms of evolution.

Darwin and Paleoanthropology

In 1871 Darwin published his second major book on evolution, *The Descent of Man*, which maybe more than all his other works "in many ways best manifests the nature of his thought" (Ghiselin 1969, p. 214). Again, he was not the first to treat this issue. In England Thomas H. Huxley (1825–1895) – "evolution's high priest" (Desmond 1997) – in his *Evidence as to Man's Place in Nature* (1863) gave forceful arguments for the descent of humans from apelike creatures and thus put us in our (right) place (Weiss 2004), and simultaneously in Germany Ernst Haeckel

(1834–1919) developed practically the same arguments. Later Haeckel published a massive book in which he extensively treated human ontogeny as well as phylogeny (Haeckel 1891). Both, Huxley and Haeckel, were enthusiastic supporters of Darwin's views from the beginning on and helped popularizing the idea of evolution by natural selection. Unlike Darwin, both were engaged in public discussions and did not avoid controversies. However, paleoanthropology, the study of fossil humans, in the 1860s and 1870s was far from being firmly established as a scientific discipline. To what extent, then, is it justified to connect Darwin with paleoanthropology? And, more generally, which role did the fossil record play in Darwin's evolutionary conceptions?

Fossils had been known already in ancient times, but were constantly interpreted as *ludus naturae* ("play of nature"), as expressions of the Creator's mood or products of the Deluge (see, e.g., Hölder 1960). The Danish physician Niels Stensen (Nicolas Steno) (1638–1687) interpreted, quite correctly, some rock-hard objects as fossil remains of ancient and extinct animals. In a way, this was the beginning of paleontology, but since Steno believed in the Deluge, his intention was to demonstrate the divine plan (Hölder 1960). Remarkably, Lamarck did not at all make use of the fossil record, for he did not believe that species can get extinct, but was rather convinced that all fossils were remnants of organisms still alive somewhere on the earth (Corsi 2011). On the other hand, his compatriot – and chief opponent – Georges Cuvier (1769–1832), who is regarded as the founder of comparative anatomy and paleozoology, did recognize fossils as traces of extinct animals but did not accept the idea of evolutionary change. Instead, he too attempted to prove the reality of the Deluge and of a short history of humans on earth (Haber 1959; Hölder 1960). That a paleontologist did not believe in evolution seems somehow amazing from the today's point of view. But Cuvier was bound to typological thinking, and besides – although he lived in a century of extraordinary paleontological activities, to which he himself contributed so much – paleontology was considered as most valuable by geologists, but its lessons for historians of life were less clear and invited controversies and opposition (Coleman 1977). Moreover, one has to be aware that fossils by themselves do not supply proofs of the evolutionary change anyway. They make plausible that the evolutionary mechanisms of the present also operated in the past (Rieppel 1984) – according to the principle of the "actual causes" that was postulated by Charles Lyell (1797–1875), Darwin's mentor and one of the founding fathers of historical geology who, after all, refuted Cuvier's "catastrophism." Yet paleontology as a historical science relies on a biological understanding of organisms, their structures and functions (Hengsbach 1979). Paleontology – as the reconstruction of extinct species – is a theory-guided discipline; without a theoretical frame the study of fossils would remain to be an art of storytelling, certainly quite entertaining, but scientifically invalid. In particular, paleoanthropologists must carefully separate "paleopoesy" from sound scientific approaches in the study of fossil humans. Their discipline is – as it always was – publicity oriented, and they have to make clear that they try to reconstruct and to conceptualize hypothetically humanity's descent (e.g., Johanson and Edey 1981; Henke 2007, 2009; Tattersall 1995, 1998; Schwartz and Tattersall 2000).

It was said that for Darwin's theoretical conceptions of evolution fossils did not play any part (Rieppel 1984). This is not true, as can be seen from previous remarks in this chapter. It is true that Darwin attained at the theory of natural selection mainly by considering other sources of information – among them and most important domestic breeding of plants and animals that he regarded as an "experiment" from which he could derive the principle of natural selection (Richards 1998) – yet he did not at all neglect the fossil record. During his *Beagle* voyage he was struck – in South America – by fossils, for example, the relics of *Glyptodon*, an extinct giant armadillo. And he collected fossils, whenever the *Beagle* anchored inshore (Huxley and Kettlewell 1965). Unlike Cuvier and Lamarck, Darwin interpreted fossils correctly as evidences for the "evolutionary chain," and his work certainly contributed much to the further development of paleontology (Schmidt 1960). In 1851 he published a monograph on fossil barnacles and in 1854 a second volume on this issue. (Probably, no other naturalist has spent so much time and energy with barnacles, extant and extinct.) This treatise alone offers ample evidence for Darwin's commitment to paleontology (see also Wuketits 2009a).

Sure, in *The Descent of Man* the references to the fossil record are scarce. But one should once again keep in mind that at that time only very few hominin fossils were known – and the few known were still controversially discussed or met with skepticism – and that it took some more years, if not decades, before paleoanthropology was established as a scientific discipline. However, what seems more important, Darwin was convinced that the lack of fossils was just due to the fact that they had not yet been discovered. He, of course, knew Huxley's seminal book *Evidences as to Man's Place in Nature* (1863) where one can find a chapter on fossil remains of humans, namely, the fragmentary skulls from the caves of Engis (Belgium) and the Neanderthal near Düsseldorf (Germany). In retrospect, Darwin had good reasons to be optimistic. In the twentieth century a vast number of fossil humans were discovered, and with their help an ever-better understanding of the evolutionary past of humans could be developed.

Why were hominin fossils at Darwin's and Huxley's time so rare? The answer is quite simple: "All the early human remains that composed [the fossil record] were incidental finds. They had turned up as by-products of quarrying or construction, of fieldworks by geologists, or of the excavations of antiquarians or prehistorians in search of artifacts" (Tattersall 1995, p. 31). Also, as should be added, for ideological reasons there was no systematic attempt to discover fossil humans for the mainstream of naturalists in the nineteenth century did not believe – or did not want to believe – in a long (evolutionary) history of humankind and was convinced of the special status of humans in nature. Thus, for example, Richard Owen (1804–1892) – a most distinguished anatomist and paleontologist and simultaneously a critic of Darwin's *Origin* – "was pulling man and ape apart, showing that moral responsibility and human freedom where altogether higher concerns" (Desmond 1982, p. 74). However, Darwin was on the right track. In his attempt to reconstruct human evolution, he could refer to data from comparative primatology, and it is astonishing how expressively he drew – irrespective of the lack of fossils – a picture of the phylogenetic relationship between humans and apes (Heberer 1960). He might be considered as the first modern anthropologist in a wide sense. His *The Descent of Man* includes full-length chapters on (human) social, moral, and intellectual capacities and outlines, in a way, what is now called evolutionary anthropology.

Paleoanthropology After Darwin: Premises and Expectations

Since in the first chapter of the present work Henke gives a comprehensive account of the history of paleoanthropology (see also Tattersall 1995), this chapter includes only a few – mainly conceptual and methodological – remarks. To begin with, one should keep in mind Tattersall's "warning": "Before you can begin to work out the relationships between extinct species in the human family, you have to have a reliable idea of how many such species there are among the many hundreds of hominid fossils known" (Tattersall 1995, p. 229). Apparently, nobody can really tell how many human species once existed because several of the alleged "species" are under discussion and not unanimously acknowledge as species. The increasing number of fossils does not automatically lead to a deeper understanding of hominization, as can be seen by the recent trend "from trees to bushes" in the representation of hominin branching (Gould 1976; Wood and Collard 1999; Tattersall and Schwartz 2000; Henke 2009). The meaning of theory must be pointed out once more: Fossils as such do not replace theory.

It is clear that the expectation of paleoanthropologists – and of anyone concerned with the evolution of humans and their position in nature – is and has always been to develop an ever-better insight into the pathways of human evolution. But expectations, when too strong, can mislead the human intellect. Like other scientific disciplines, the history of paleoanthropology includes examples for such misguidance.

Again, the Piltdown forgery has to be remembered. "Piltdown man," *Eoanthropus dawsoni* – literally, the human of the aurora – was considered for 40 years as an evidence for the roots of humans in Europe. In a comprehensive paleoanthropological work, Keith (1925) devoted almost 200 pages to the description and explanation of this "fossil document" that, as he enthusiastically stated, "is the most important and instructive of all ancient human documents yet discovered in Europe" (Keith 1925, Vol. 2, p. 486). The interpretations of the Piltdown skull were somehow adventurous but very promising – "the first female intellectual" (Hooton 1947, p. 306) – and were guided, in the last (if not in the first) instance, by ideology. *Eoanthropus* was used to prove the European origin of humans. While already Darwin (1871) had assumed that Africa was the cradle of humankind, all those anthropologists who embraced (almost in a literal sense) the Piltdown skull could not – or did not want to – acquire a taste for an "out-of-Africa hypotheses." Later Darwin's suggestion was substantiated by the fossil record ranging from the Oligocene to the Pleistocene (Leakey 1960), and up to now no unobjectionable support has been found for an opposite view.

"Nebraska man," *Hesperopithecus haroldcookii*, is a story somewhat even more curious than its British counterpart (see Gould 1989). About 10 years after the Piltdown "discovery," a single tooth was found in Nebraska and finally interpreted as the relic of a higher, manlike primate that could demonstrate the early ancestry of humans in North America. This time, however, it did not take long to recover the truth: The tooth turned out to be a remnant of an extinct species of peccaries, piglike animals now around in the south of the United States, in Central America, and in northern regions of South America. Unlike the Piltdown skull this fossil was not a forgery, but as in the former case, it apparently had aroused some ideologically motivated hopes.

Like in any other scientific discipline research work in paleoanthropology leaves some room for speculations, but one must distinguish between wild and sound speculations (Bunge 1983). The discovery of hominin fossils depends on several factors, for example – if not above all – a sophisticated planning of excavations. But sometimes such plans do not really help much; not every excavation brings sensational fossils to light. Sometimes paleoanthropologists have simply good luck, so that it does not come as a surprise that the mass media often treat new discoveries like nuggets. Like all scientists, paleoanthropologists are usually very ambitious, and it is quite natural that they are also driven by emotions. Behind the scenes of the search for human origins, then, they can be found engaged in personal animosities and displaying different typically human patterns of behavior (see Lewin 1987). As the late David L. Hull in a long book on the process of science stated: "The objectivity that matters so much in science is not primarily a characteristic of individual scientists but of scientific communities. Scientists rarely refute their own pet hypothesis" (Hull 1988, pp. 3–4). But Hull (1988, p. 4) also considered that "science is so structured that scientists must, to further their own research, use the work of other scientists. The better they are at evaluating the work of others when it is relevant to their own research, the more successful they will be." This means that, in a sense, scientists are forced to cooperate. With respect to hominin fossils and their interpretations, paleoanthropologists would have hardly attained at the present understanding of human evolution, if all of them would have automatically disagreed with everything and anything that others had achieved, be it at the empirical or at the theoretical level.

But another and somehow sensitive point is to be mentioned here. Certainly, the search for their own ancestry is the most fascinating intellectual adventure that humans can undertake. As history shows, the picture that humans developed about themselves has changed, and it has differed from one culture to another. But everywhere and at any time, one finds some ideas on the origin of humankind. Paleoanthropologists are therefore well advised to consider that they "fulfil needs that are reflected in the fact that all societies have in their culture some form of origin beliefs, that is, some narrative or configurational notion of how the world and humanity began" (Isaac 1983, p. 509). It is therefore important to point out – in the public – that paleoanthropology does not tell just another story about human origins, but that its premises and goals are grounded in a way of thinking which is completely different from that of myths. Moreover, paleoanthropology is not the search for documents that give evidence for the special status of humans in nature that some tried to harden even in the second half of the twentieth century (e.g., Hofer and Altner 1972); its aim is rather (hand in hand with primatology) to close the long supposed gap between humans and other animals.

Unlike paleobotanists and paleozoologists, paleoanthropologists are confronted with a psychological aspect, which means that they are operating with humanity's self-image (Lewin 1987). The broader audience of paleontologists is of course more concerned about the origin and evolutionary history of humans than it is fascinated by fossil rats, dragonflies, or crinoids (dinosaurs and perhaps mammoths and other "giants" are maybe exceptions). Also, paleoanthropologists are challenged by the old question "What is man?" and thus encounter the problem, which of their findings are to be characterized as "human." Where to draw a line between humans and nonhumans? Is it at all possible to draw such a line? (Junker 2006).

One cannot seriously expect that sooner or later paleoanthropologists will have a completed (fossil) record of human evolution. "In fact," says Tattersall (1995, p i), "we will never have a human fossil record that preserves even one thousandth of one percent of all the individuals that have ever lived." But this should not be a reason for discouragement, because, as Tattersall continues, "even now we have a reasonably good sampling of fossil species – even fossil human species – that should allow us, by appropriate analysis, to gain a provisional idea of the major events that led to the emergence of our own kind on Earth." The question only is to which extent we are – and will be – able to arrange this "good sampling" to a coherent picture of our evolutionary past. Again, one comes to the meaning of theory in paleoanthropology. Here – for historical, disciplinary and substantial reasons – one theory deserves particular attention: synthetic theory.

Synthetic Theory or Modern Synthesis

The Rise of an Influential View of Evolution

Synthetic theory or modern synthesis, the "second Darwinian revolution" (Junker 2004), has been one of the most successful theories in the biological sciences, and its formation, influence, and implications have already been subject of numerous historical and methodological studies (see, e.g., Bowler 1984; Junker 2004; Reif et al. 2000; Smocovitis 1992; Wuketits 1984, 1988). The theory grew from Darwin's theory of natural selection and outgrew it with regard to empirical data and explanatory power. Briefly, its main achievements can be summarized as follows:

- The theory is "synthetic" (or pluralistic) in the sense that it offers a multifactor analysis and explanation of evolution combining selection, genetic recombination, mutation, (geographically induced) reproductive isolation, and changes in population size.

- It is a "synthesis," because it refers to findings and concepts in practically all fields of biological research, from anatomy to ecology and biogeography and from genetics to paleontology, and makes also use of data from other disciplines such as geology and oceanography.
- Within the frame of synthetic theory, the factors or mechanisms analyzed at the level of microevolution fully apply to – and sufficiently explain – macroevolutionary processes.

Generally, one can say that synthetic theory has put evolutionary theory in the center of biological sciences – as the theory to which all aspects of the study of organisms have to be referred. In the words of Julian Huxley (1887–1975), one of the founding fathers and chief proponents of synthetic theory: "The evolutionary approach will prompt us to ask the right questions of nature, and, when we have asked them, will help us to find the right answers" (Huxley 1958, p. 23). This might sound somehow prophetic but proved to be completely true.

Huxley's *Evolution, the modern synthesis* (1942 [reissued 2010]) introduced the synthetic theory as a broad concept of evolutionary thinking and is to be regarded as a cornerstone in the history of evolutionary theory. If, however, one wants to understand the rise – and final success – of synthetic theory, one has to take into account that up to the 1930s there was practically no agreement concerning the treatment of evolutionary questions. Therefore, even when in 1947 a conference on evolution was organized by the "Committee on Common Problems of Genetics, Paleontology, and Systematics" of the National Research Council, commentators were astonished that the discrepancies between several fields dealing with evolution that had dominated discussions for several decades had practically vanished (Reif et al. 2000). In fact, the status of evolutionary theory in the first decades of the twentieth century was rather blurred, and issues like genetic mechanisms of evolution were controversially discussed. There were several rival theories, for instance, to mention just two, the "mutation theory" by the Dutch plant physiologist and geneticist Hugo de Vries (1848–1935) and "neo-Lamarckism" (actually a name for a bundle of theoretical conceptions). This is not to say that with the emergence of the synthetic theory, really all controversies came to an end, but this theory was a major contribution to unifying biological concepts.

Progress in any scientific discipline is made if – and only if – more and more separate data and concepts are brought together and combined in a broad theory. In the case of evolutionary biology, Darwin synthesized all biological disciplines that were established at his time, but he had – as should be remembered – only very vague ideas about genetics. In more harsh words: "He knew nothing about the causes of hereditary variation, and his opinions on this subject were neither logical nor consistent" (Stebbins 1971, p. 11). The result of this deficiency was his rather nebulous concept of "pangenesis," which was based on Lamarckian principles. He was unaware of the work of Gregor Mendel (1822–1884) whose discoveries would have been quite important for him, but Mendel generally, for some decades, did not receive any attention. Only at the beginning of the twentieth century his "laws of heredity" were rediscovered (by de Vries and other researchers). More or less simultaneously, the German zoologist August Weismann (1834–1914) embarked upon a synthesis in evolutionary biology. Initially a Lamarckian, he combined cytology, embryology, and (Mendelian) genetics with the theory of natural selection (see Sander 1985). The result was "neo-Darwinism," an expanded version of Darwin's evolutionary conceptions which could be brought to a simple formula: Darwin's theory of natural selection plus classical (Mendelian) genetics. For historical and terminological reasons, it has to be pointed out that neo-Darwinism must not – as frequently happens (see, e.g., Ruse 1982) – be confused with synthetic theory (Reif et al. 2000; Wuketits 1988). The step done by the advocates of synthetic theory was to enhance genetics – from Mendelian genetics to population genetics.

Several authors contributed – at the beginning more or less independently of each other – to the formation of the modern synthesis. As was mentioned above, Julian Huxley published the first full-length book already in its title explicitly referring to a (new) synthetic view of evolution. Remarkable contributions to this view followed.

A leading and ardent proponent of the synthetic theory for some 60 years was Ernst Mayr (1904–2005), who is sometimes called "Darwin of the twentieth century" (see Bock 1994; Greene 1994; Smocovitis 2007). Mayr was a trained ornithologist and systematist, but throughout his career also concerned with history of biology and later with philosophical questions in the life sciences. An indefatigable writer and commentator, he frequently pointed out the importance of historical narratives in biology and used the structure of evolutionary theory to demonstrate the autonomy of biology among the natural sciences (see, e.g., Mayr 2004; Wuketits 2004). Mayr has been criticized, from time to time, as being dogmatic, and it is true that already in the late 1950s he "talked about the Synthetic Theory as something completed" (Reif et al. 2000, p. 47). Since he was lucky to reach a very old age, he watched the evolution controversies – and contributed to them – for many decades. He performed much to popularize Darwin and evolution in general and published, at the age of 97, a fresh and accessible book on major evolutionary issues from the point of view of a Darwinian (Mayr 2001).

From the perspective of genetics, it was Theodosius Dobzhansky (1900–1975) who in his *Genetics and the Origin of Species*, first published in 1937, authoritatively contributed to the formation of the synthetic theory. This work can probably be regarded as the first expressive presentation of the synthetic theory, although its author did not use this word. However, it was not by chance that Huxley in his *Modern Synthesis* frequently referred to it and to other of Dobzhansky's writings. It seems that when Dobzhansky, a born Russian, moved to the United States in 1929, his genetically informed ideas of evolution were already most advanced (Brito da Cunha 1998). Like Mayr, Dobzhansky was interested in philosophical questions, too, but unlike Mayr and the other architects of the synthetic theory, he was – somehow amazingly – a Christian believer.

George G. Simpson (1902–1984), in contrast, bluntly expressed his unbelief and his commitment to rational, scientific thinking. "It is possible," he remarked, "that some children are made happy by a belief in Santa Claus, but adults should prefer to live in a world of reality and reason" (Simpson 1963, p. 25). Simpson was a paleontologist, and his chief contribution to the modern synthesis was *The Major Features of Evolution* (1953), a book that was preceded by numerous of his other writings. It was said that Huxley's *Modern Synthesis* was not just a contribution to evolutionary theory in a strict sense but "was also to act as a remedy for the ills of the modern world" (Smocovitis 1992, p. 33). Similar statements could be made on Simpson's work. The paleontologist was not confined to paleontological data and their arrangement but was also concerned with the destiny of humans. Man is just a species of primate, he said, but "among the myriads forms of matter and of life on the earth, or as far as we know in the universe, man is unique. He happens to represent the highest form of organization of matter and energy that has ever appeared" (Simpson 1958, p. 179). However, he never lost interest in paleontology as a field discipline, and late in his life he published a readable book on fossils in which he also treated fundamental questions of evolution (Simpson 1983).

Like Simpson, Bernhard Rensch (1900–1990), the chief German proponent of the synthetic theory who was internationally recognized, dedicated much time and many of his publications to explain the special status of humans. Rensch was a polymath in biology, and he was also well informed in the fields of history, psychology, and – particularly – philosophy (see Wuketits 2006). His major contribution to the formation of the synthetic theory, *Neuere Probleme der Abstammungslehre* (Rensch 1972), was first published in 1947, revised in 1954 and 1972, and English editions – entitled *Evolution above the Species Level* – were published (1959, 1960) in London and New York, respectively. Mentioning this translation is not unimportant for the publications of some other German representatives of the synthetic theory appeared invariably in German and were not – or only to a minor extent – perceived in the English-speaking world. This applies to Gerhard Heberer (1901–1973) and Walter Zimmermann (1892–1980).

During his lifetime Heberer was, in German speaking countries, probably the best known anthropologist or paleoanthropologist for that matter. This is not the place to discuss his Nazi entanglement, but it should be stressed that Heberer for decades had been engaged in the reconstruction of human history and regularly published provisional pictures (*Jeweilsbilder*) of the understanding of human evolution as documented by the fossil record. Among his last publications are two books (Heberer 1968, 1972), the first a popular account of the evolution of hominids and the second a somewhat more technical, but accessible, small volume. After his death this volume was expanded by Henke and Rothe (1980). Also, Heberer edited a comprehensive book on the evolution of organisms that first appeared in 1943 and later, in the 1960s and early 1970s, in three volumes. The work is to be regarded as a testimony of synthetic theory and of the validity of Darwinian views applied to the reconstruction of evolution and was "the most comprehensive statement of the Synthesis that was published during its formation phase in Germany" (Reif et al. 2000, p. 73). Heberer also edited an extensive volume on the advances in the understanding of human evolution (Heberer 1965).

Zimmermann was a paleobotanist but generally interested in evolutionary questions. He published a well-documented book on the history of evolutionary thinking up to the mid-twentieth century (Zimmermann 1953) and another volume in which he – in a (more or less) truly neo-Darwinian tradition – attempted to refute the Lamarckian assumption of an inheritance of acquired characteristics (Zimmermann 1969). Also, he was concerned with the methodology of phylogenetic reconstructions and the philosophy of evolution, as his – somehow positivist and thus, from today's point of view – obsolete volume on these issues shows (Zimmermann 1968).

Sure, one should mention some other contributors to the synthetic theory – they are named, for example, by Reif et al. (2000) and Smocovitis (1992) (see also Junker 2004, on references to German authors) – but in the present context, the reference to the here mentioned naturalists may suffice. All of them were interested in human evolution and treated philosophical issues on this topic. All of them tried to explain the appearance of humans in a way that Darwin had sketched and were convinced that the previously, from ancient times on formulated enigma of the very human being could be resolved in terms of evolution by natural selection. Nothing can be said here about disagreements among the advocates of the synthetic theory. What is more important in the present context is the general success of the modern synthesis which is also due to the fact that their architects seemed to form something like a phalanx and "seemed tacitly to have agreed to play down their differences and to emphasize their areas of agreement" (Hull 1988, p. 201). The reason for this "agreement about agreement" was maybe a philosophical one: the goal to establish a secular, materialist world view, to give a definitely naturalistic account for the human species, and so finally to dismiss – in Darwin's spirit – the long-lasting idealist tradition. Tattersall (2000, p. 2) wryly remarks that the synthetic theory "was doomed to harden, much like a religion, into a dogma." Especially Mayr has been from time to time accused to be too dogmatic, but he used to say that even he was dogmatic, he did good service to the theory: People frequently react quite sensitively to dogmatically defended positions and try to refute them; this way, a theory can be tested and improved. Sure, no scientific theory should be defended and preached like a dogma. What counts, after all, is its explanatory power. And one must admit that the explanatory power of the modern synthesis has been quite noticeable – and that the advocates of the synthetic theory have stimulated further discussions and opened doors to additional critical studies on the patterns and processes of evolution.

The success of the synthetic theory must not obscure the fact that at least some of its tenets and implications were exposed to criticism "from outside" the theory. Thus, at an international conference on evolution held in Halle an der Saale (Germany, at that time German Democratic Republic) in October 1973 Mayr expressed his conviction that all questions of evolutionary change can be sufficiently resolved within the frame of the synthetic theory, while Remane was much less optimistic and rather critical (Mayr 1975; Remane 1975). Adolf Remane (1898–1976), one of the most influential zoologists for several decades in twentieth-century Germany, opposed to synthetic theory for different – maybe also personal and political – reasons (Junker 2000). It appears that his main drive to resist synthetic theory was his sympathy for the traditional German morphology that – to a certain extent even in the twentieth century – was guided by a typological approach to nature. The same is probably also true to the German paleontologist Otto Heinrich Schindewolf (1896–1971) (see section "Synthetic Theory and Paleontology, Particularly Paleoanthropology").

Despite some disagreements, the architects and early advocates of the synthetic theory had come to terms at least about two aspects. First, they did not see any serious gap between microevolutionary and macroevolutionary processes, and, second, they fostered an adaptationist program, i.e., the view that any trait of organisms in the last instance can be explained in terms of adaptation. How seriously they took this program can be seen from their different books mentioned in this section (e.g., Dobzhansky 1951; Mayr 1963). Therefore, the proponents of the synthetic theory generally rejected – among other conceptions like goal-oriented evolution and types (*Baupläne*) – the notion of an autogenetic, autonomous evolution without interaction with the environment (Reif et al. 2000).

Synthetic Theory and Paleontology, Particularly Paleoanthropology

Few of the leading figures of the synthetic theory were professional paleontologists or paleoanthropologists. Most influential among them was Simpson; less influential were Heberer and Zimmermann. However, already a glance at the major works on synthetic theory in the 1940s and 1950s reveals that their authors paid significant attention to paleontology, although the importance of this discipline is not always explicitly underlined and in some writings said to be quite limited. Huxley (1942, p. 38), for instance, stated that paleontology can only "assert that, as regards the type of organisms which it studies, the evolutionary methods suggested by the geneticists and evolutionists shall not contradict its data." But since the advocates of the synthetic theory anyway did not wish discrepancies between the data of different (biological) disciplines, this statement appears to be trivial.

The main concern on paleontological ground was to refute saltationism, the idea that evolution occurs discontinuously, as was supposed, for example, by Schindewolf who used the term "typostrophe" (in analogy to "catastrophe") to indicate discontinuities in evolutionary change in the case of the emergence of higher taxonomic groups (Schindewolf 1950). Schindewolf stood in an old tradition reaching way back to the nineteenth century when the lack of fossils was received well by all those who generally – and often enough for ideological reasons – opposed to evolutionary thinking. He was definitely not skeptical about evolution as such (see also Schindewolf 1972) but argued against gradualism.

On the other side, Simpson (1953, p. 103) accurately stated: "The paleontological evidence for discontinuity consists of the frequent sudden appearance of new groups in the fossil record, a suddenness common to all taxonomic levels and nearly universal at high levels. Since the record is, and must always remain, incomplete, such evidence can never *prove* the discontinuity to be original."

Yet the controversy "continuity vs. discontinuity" or "gradualism vs. saltationism" endured. The gradualist model implicitly accepted by many advocates of the synthetic theory was challenged in the early 1970s by the concept of "punctuated equilibria" (Eldredge and Gould 1972) that accounts for rapid evolutionary changes. However, it now seems that the case is finished for evolutionists meanwhile tend to agree that evolution occurs at different speeds. The gradualist model still applies to many lineages, and the punctuational model applies to others. In retrospect, the controversy "gradualism vs. punctualism" may seem as an artificially induced debate, because already Simpson (1953, p. 313) clearly had stated that "it is abundantly evident that rates of evolution vary. They vary greatly from group to group, and even among closely related lineages there may be strikingly different rates." In other words, if one wants to find examples for gradualistic change, he or she will easily find them, and the same is true to the punctuational model. Human evolution, by the way, seems to be a good example for the latter, especially if one keeps in mind the comparatively rapid increase in brain size at the level of the genus *Homo*.

Although with the exception of Heberer practically none of the early – and leading – advocates of the modern synthesis was a paleoanthropologist by profession, most of them were, as was already indicated, interested in human evolution and concerned with the place of humans in nature. Dobzhansky published *Evolution, Genetics, and Man* (1957) which includes a long chapter of human evolution, and Rensch (1970) devoted a book explicitly to the pathways leading to *Homo sapiens*. (It is, maybe, worth mentioning that Dobzhansky's book was translated into German and that Rensch's work appeared in English translations in Great Britain as well as in the United States.) Mayr's influential *Animal Species and Evolution* (1963) (which was published in German as well) also includes a chapter of man as a biological species, and Julian Huxley was dealing with human evolution throughout his career anyway. In his later years he was engaged in developing and propagating a secular evolutionary humanism (see, e.g., Huxley 1966). All these works had a common aim: to demonstrate that the paths and mechanisms of evolution reconstructed within the frame of synthetic theory on the basis of Darwinian views fully apply to humankind, albeit their authors presumed the uniqueness of *Homo sapiens*. They referred to paleoanthropological data on a more or less large scale and left no doubt that they – in Thomas Huxley's tradition – considered evidences as to man's place in nature of crucial importance. Also, all of them were attracted by philosophical issues (which is not really surprising because of their classical education).

The Modern Synthesis and Beyond

The mentioned adaptationist paradigm inherent in the synthetic theory has aroused much discomfort and criticism, for one could get the impression that when bringing this paradigm consequently to an end organisms appear to be rather "passive objects" structured merely by their environment(s). Thus, Gould and Lewontin (1978) somehow ironically compared the adaptationist program to a “panglossian paradigm” and pointed to its failure to conceive of evolution as a process with passive organisms instead of seeing living systems as integrated wholes with specific constraints delimiting pathways of (evolutionary) change and therefore being more interesting that environmental selection. In other words, the extent of evolutionary changes, their particular direction, and the degree of adaptation as a result of these changes are largely determined by the organisms themselves. “Selection may supply all immediate direction, but if highly constraining channels are built of nonadaptations, and if evolutionary versatility resides primarily in the nature and extent of nonadaptive pools, ‘internal’ factors of organic design are an equal partner with selection” (Gould 1982b, p. 384).

Such factors were expounded, with some insight, by the Viennese zoologist Rupert Riedl (1925–2005) as integral parts of what is called “systems theory of evolution” (Riedl 1975, 1977; Wagner 1986; Wuketits 1988). It must be pointed out that “internal factors,” as already proposed by Whyte (1965) and before by some other writers, do not resemble the cryptic vital forces that were postulated in earlier times – up to the twentieth century – by advocates of vitalistic doctrines. Rather, within the corpus of systems theory, “internal factors” mean organismic constraints, i.e., the sum total of organizational and functional principles that limit an organism’s adaptability to its outer world. To put it the other way, adaptability is not – and cannot be – defined by the organism’s environment, but by the organism itself. It is not by chance that the systems approach to evolution includes data and conceptions from developmental biology. Ontogenetic constraints have meanwhile received much attention by many evolutionists and have been considered as elements of a new and broader evolutionary synthesis (see, e.g., Müller 2005; Pigliucci and Müller 2010). Generally, one can say that up from the 1970s there have been attempts to establish a broader, organismic view of evolution that somehow transgresses synthetic theory and its explanatory power. This view – without opposing the basic premises of Darwinism and the modern synthesis – lays particular stress to organisms as active systems. For this reason it might be also called “active Darwinism” (Perutz 1986). In retrospect, the question posed by Stebbins and Ayala (1981) whether a new evolutionary synthesis is necessary can be answered by “yes,” but most important steps towards such a synthesis have already be done. Natural selection as external selection has been supplemented by internal selection, and evolution appears to be a complex interaction between inner and outer selective forces. Organisms themselves play a crucial role in their own evolutionary change, and a comprehensive organismic or systems approach to evolution puts living beings in the center of evolutionary thinking.

Remarkably, Darwin was already aware that natural selection, understood as a mere outer factor of evolution, is not enough to explain the existence of particular complex characters of organisms. He deliberately stated: “Naturalists continually refer to external conditions, such as climate, food, etc., as the only possible source of variation. In one limited sense . . . this may be true; but it is preposterous to attribute to mere external conditions, the structure, for instance, of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees" (Darwin 1859 [1958], p. 28). One can say that Darwin had in mind intraorganismic constraints and that he by no means underestimated the role of the organism in evolution (see also Wuketits 2000).

The estimation of internal selection is of particular importance to paleoanthropology. When reconstructing fossil Hominini, paleoanthropologists must always be aware that the organisms which they are trying to understand within their specific "life worlds" were not just molded or "modeled" by external forces, but rather influencing their own environments to a certain degree. The evolutionary success of the genus *Homo* is to a considerable extent certainly due to the fact that it was more and more able to cope with challenges in its environment(s) and to control "environmental forces." Reconstructing, recognizing, and defining the genus *Homo* have troubled paleoanthropologists for decades (Collard and Wood, this handbook, vol. III; Henke 1981, 2005; Henke and Hardt 2011; Henke and Rothe 1999; Howells 1966; Rothe and Henke 2006), yet there can be hardly any doubt that this genus – now represented by the single species *Homo sapiens* – has been a "careerist," a "born winner," so to speak. Undoubtedly, it is highly adaptable, but many if not most of its achievements are due to its ability to get some control over its environment.

To summarize briefly to this point, evolutionary theory has turned out to be the only serious and reliable explanation of the staggering diversity of life on earth including humans, but it has – as is quite "normal" in the case of scientific theories – undergone some changes. Ever since Darwin new empirical findings have been made and his theories profited from controversies. The synthetic theory or modern synthesis has been a truly multidisciplinary approach to study evolutionary phenomena, and as a pluralistic theory regarding the factors of evolution, it has explained a vast number of details that, when viewed separately, appear somewhat enigmatic in character (e.g., geographical variation, genetic assimilation, and many others). Yet the synthetic theory gave rise to controversies and so an even broader theory of evolution emerged. Advances in evolutionary thinking have had always some (positive) impact on the study of human evolution, as on the other side paleoanthropology has inspired general reflections on evolutionary change. Despite all the open questions concerning many details of life's history, one can now state that the evolution of humans is not to be regarded as a "special case" of evolution, but that it fits into the general principles so far known as "mechanisms of evolution."

Anthropology: The Need for Synthesis

"Anthropology, the study of humankind, seeks to produce useful generalizations about people and their behavior and to arrive at the fullest possible understanding of human diversity" as one reads in the preface of a comprehensive, 700-plus page textbook on anthropology (Haviland 1985, p. 7). This "definition" of anthropology seems trivial – what else could the study of humans be! However, one has to recognize the present status of anthropology: The discipline is split into a vast number of specialized fields that have developed their own methodology and terminology. A synthesis is urgently needed. It can be argued that paleoanthropology is a very good way to establish this synthesis.

Paleoanthropology is part and parcel of evolutionary thinking and has influenced evolutionary theories in different ways. Paleoanthropologists have to take into account not just fossil remains of humans but data and conceptions from different disciplines such as geology, biogeography, primatology, archaeology, and others (see Henke 2005; The history of Paleoanthropology). As a theory-guided discipline, paleoanthropology also fulfills the standards of modern philosophy of science: Single "facts" are not enough; they have to be embedded into a theoretical framework (chapter "▶ Evolutionary Theory in Philosophical Focus," Vol. 1). Unfortunately, as it seems, many anthropologists have abandoned the very goal of their discipline: an understanding of humans, their history, their present status, and their possible future. Sure, for many centuries the study of humans was strongly influenced by idealistic philosophy and by the attempt to demonstrate the special status of humans as creations of God. On the other hand, one should not neglect the efforts of anthropologists during the past 200 years or so – especially after Darwin – that gradually offered a quite profound understanding of our species in the evolutionary process. The advances that paleoanthropology has made more recently can be seen when one compares reviews from the mid-1980s (e.g., Pilbeam 1984) with newer ones (e.g., Tattersall and Schwartz 2000; Henke 2005, 2009).

Despite all the debates about the number of fossil hominin species and problems of systematics, taxonomy, and classification (see, e.g., Cela-Conde 1998), paleoanthropology is unmistakably well established as a scientific discipline. Anthropologists who study very specialized traits of particular (recent) human populations should see good reasons to ask, to which extent such traits could be seen as parts of more general trends in human evolution. Otherwise anthropology runs the risk to come to the level of an aimless collecting of stamps. Stamp collection as such is quite interesting and entertaining, but the "true" collector wants to know something about the origin and meaning of his material and is inclined to study the history of stamps in connection with other historical events. Anthropologists should always keep in mind the two fundamental questions of any evolutionary approach. First, where does a particular trait – be it an anatomical structure, a pattern of behavior or whatever – comes from, i.e., what are its evolutionary origins? Second, what is the biological purpose or advantage of any particular trait? Hence, after all, anthropologists in first and last instance have to refer to evolutionary theory.

The now growing discipline of evolutionary anthropology demonstrates how different aspects of human life can be explained on the ground of evolutionary thinking. Bringing together data and concepts from several disciplines and integrating them into a conceptual scheme, evolutionary anthropology can show the way towards a new anthropological synthesis. Paleoanthropology will be an important part of such a synthesis.

Much light has already been thrown on the origin of humans and their history.

Conclusion

Despite some earlier speculations on the changeability of species (Buffon, Diderot, and others), evolutionary thinking – as theory in a strict sense – was not established before the nineteenth century (Lamarck, Darwin). It replaced a bundle of traditional views of the world that are deeply rooted in Western philosophy: static conceptions of nature, typological thinking, and Act of Creation according to the Old Testament. Among other explanations of the processes of evolution Darwin's theory of natural selection proved to be generally the best approach. However, in the twentieth century is was rectified and extended to a more comprehensive view of evolution, the synthetic theory or modern synthesis which recently was again extended to a broader, organismic conception (systems theory). Some of the crucial problems, particularly whether evolution has occurred by gradation or in a saltationist way, are now practically solved.

From its very beginning on the theory of evolution included statements on the position of humans in nature and their possible descent from other, "lower" creatures. Darwin (1871) argued that there cannot be any doubt that humans carry in themselves traces of their "lower ancestry." The advances of paleoanthropology during the past 100 years or so gave him right. The study of fossil remains of humans – no matter that it is still incomplete (and most probably will remain incomplete in the future) – shows that human evolution can be reconstructed on principle grounds. Most important has been the insight that fossils as such do not tell the story of human evolution. They have to be interpreted, connected with findings in different disciplines, and linked to evolutionary theory. The same is, of course, also true to fossil remnants of all other organisms, be they oak trees, scorpions, sharks, rodents, or elephants. Yet studying the fossil record is indispensible to any attempt to reconstruct the history of life including humans.

"Within a multidisciplinary and multifaceted approach, paleoanthropology tries to decipher the adaptive problems that have been important in human evolution" (Henke 2005, p. 117). "Adaptation" does not, as was mentioned, mean that humans have simply been molded by their respective environments but should be interpreted – to put it briefly – in the following way: In close interaction to their environments, humans have been able to find solutions for their problems of life, i.e., to handle their life's requirements. As the preceding expositions demonstrate, adaptationism in its strict sense has been replaced by a more organism-oriented view that fully – and particularly – applies to humans.

Paleoanthropologists – as far as they take evolutionary thinking really seriously – do no longer try to find out the special status of humans in nature, but apply the methods and principles of reconstructing extinct animals, particularly mammals, fully to the deciphering of fossil humans. They should not, however, pursue their goals monomaniacally, but realize that "improvements in knowledge about human evolution require the acquisition of richly diverse classes of information" (Isaac 1983, p. 538) and that there is an urgent need of synthesis. This need concerns anthropology as a broader field of studying humans. It was one of the targets of this chapter to point to the necessity of synthetic approaches.

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Evolutionary Theory in Philosophical Focus

Philippe Huneman

Contents

Abstract

This chapter surveys the philosophical problems raised by two Darwinian claims: the existence of a “tree of life” and the explanatory power of natural selection. The first part explores philosophical issues concerning the process of evolution by natural selection. After laying out the nature of selectionist

P. Huneman (✉)
Institut d’Histoire et de Philosophie des Sciences et des Techniques, CNRS/Université Paris I Sorbonne, Paris, France
e-mail: philippe.huneman@gmail.com

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explanations, their conditions, and some of their correlated properties such as fitness, we present the epistemic issues raised by such explanations. These include the role of optimality considerations and dynamical modeling, as well as the respective contributions of analytical explanation and historical narratives to evolutionary understanding. Then the metaphysical aspects of natural selection are examined: whether it is a law or supports natural laws; whether it is a cause, and if so, the cause of what. The consequences of the answers to these questions for scientific practice, and especially for current controversies about a possible extension or revision of the Modern Synthesis, are highlighted. The chapter then presents two classical controversies regarding the target and the limits of selective explanations – units of selection, adaptationism – in both cases pointing out the promises of explanatory pluralism. The third section considers issues raised by evolutionary patterns: first, the interpretation of the nodes in the tree of life, where the notion of species is controversial; then, the question of the relationship between macro- and microevolution, and, relatedly, the connection between putative processes and plausible patterns. Consequences for the current controversy about the fate of the Modern Synthesis are also explained. We further explicate issues raised by general features of large-scale phylogenetic patterns, such as increases in complexity, and the question of evolutionary contingency, and discuss the chances of an empirical solution to these longstanding puzzles. The last section considers some consequences of evolutionary theory for philosophical questions about human nature, given the rise of hypotheses on the universality of selectionist explanations; it is mostly concerned with epistemology and psychology.

Introduction

The Darwinian theory of evolution provides a framework of explanatory strategies to explain diversity and adaptation in the living realm. Darwinian science suggested and justified two main claims: first, the existence of a "tree of life," meaning that all extant living species are the historical results of common descent, and second, the *selection hypothesis*, meaning that one of the most important processes to account for those transformations is "natural selection." Hence, Darwin's theory added to the earlier life sciences a new *explanandum* (object to be explained) – phylogenesis – and a new *explanans* (way to explain) – natural selection – the latter of which could also serve as an explanatory device when applied to existing problems in those fields. The concept of evolution, then, having been solidly grounded in that of natural selection, could in turn explain aspects of diversity and adaptation.

Of course, the full consequences of Darwin's two main claims were not recognized immediately; people were too much concerned with the two metaphysical antipodes of evolution versus creationism, and with the animal origins of man. It took almost a century to acquire the historical distance that enables us to fully appreciate the novelty of Darwinism. (On progressive extensions of Darwin's theory, see Ospovat (1981) and Bowler (1989).) In the late nineteenth century

August Weismann, by distinguishing between soma and germ line and postulating that there was no transmission of acquired characters, clarified the difference between Darwinism and Lamarckism and convinced his followers to regard only the germ line as the substrate of evolution, enabling the future integration of genetics with evolutionary biology. Weismann also demonstrated the impossibility of the theories of heredity and variation held by many biologists at the time, including Darwin himself, according to which hereditary traits could arise from within an individual organism's cells and flow continuously from them.

Heredity was a major theoretical problem for Darwinism after Darwin. After 1900, the Mendelians supported "particular" inheritance – i.e., inheritance conceived as the transmission of discrete "determinants" of traits, later to be called genes, which are randomly taken from the two parents in the case of sexual reproduction. This notion contrasted with the traditional concept, shared by Darwin, of a "blending inheritance," according to which the offspring receives a mix of the values of the traits of each parent. Blending inheritance is problematic for Darwinism because it seems that with each generation change, the "best traits" – the ones that give the most advantages to their carriers – are diluted or lost in the mixing (except in the very improbable scenario where these carriers always mate with other carriers of the advantageous traits).

Population genetics was developed in the 1920–1930s, especially by Ronald Fisher, Sewall Wright, J.B. Haldane, and Julian Huxley, as the science of the variation of gene frequencies in a population. Research in this field has shown that in the case of Mendelian inheritance, even a slightly advantageous gene will indeed increase in frequency in a population until its fixation. More generally, population genetics provided biologists with a mathematical model of the process of evolution by natural selection. Whereas previously, the Mendelian vision of organisms as mosaics of traits seemed to contradict the gradualist view of evolution as a kind of "continuous transformation" (Gayon 1998), the population genetic approach was now able to conciliate Mendelian genetic inheritance and Darwinian evolution, resulting in the form of evolutionary theory called the *Modern Synthesis*. (Mayr and Proine 1980)

For this reason, population genetics holds a central status within evolutionary thinking, as indicated by the textbook definition of evolution as the "change of allele frequencies in the gene pool," which clearly pertains to the field of population genetics. This central role of this field is not unanimously accepted today: many biologists, especially some of those working in the tradition of developmental theory and some ecologists, criticize the very framework of the Modern Synthesis, arguing that it leaves aside many important aspects of evolution, in particular developmental processes. Calls are being made for an "extended synthesis" (Müller and Pigliucci 2011) – by which is meant, among other things, that the process of evolution should be assumed to extend beyond the genes themselves (for instance, it should include cases of non-genetic inheritance that have recently been established and studied; e.g., Danchin et al. 2011 or it should include the molding of environments by organism themselves called niche-construction, Odling-Smee et al. 2003). But actually, many proponents of the Modern Synthesis, such as Simpson and Mayr, were not convinced themselves by its narrow definition.

Labels aside, it seems important to ask whether allele frequency change *constitutes* evolution, *causes* evolution, or just *indicates* evolution. This philosophical issue appears to be at the heart of the interpretation of evolutionary theory and the assessment of any alternatives to the Modern Synthesis – which shows that, in the case of evolutionary biology, philosophical aspects are intertwined with contemporary scientific controversies, as this chapter will argue in detail.

In order to grasp the new kinds of epistemological problems brought about by the two Darwinian contentions, it is useful to recall the features of the earlier biological framework that they replaced. The main *explanans* of diversity and adaptation before Darwin was, as we know, the notion of divine design, although alternative hypotheses were increasingly being proposed, especially the transformist theory of Lamarck, which was adopted by Saint Hilaire and many morphologists at the beginning of the nineteenth century. This design was invoked to account for some *prima facie* teleological features of the living world, such as the fine adaptation of organisms to their environment, the fine-tuning of the mechanisms of biological functions, or the proportions of individuals in various species and the geographical relationships between species. Divine design yielded simultaneously the *individual designs* of organisms, unlikely to be produced by the mere laws of physics, and the *design of the entirety of nature* that Linnaeus called the "economy of nature." The selection hypothesis gave a powerful explanation of those two designs, since adaptations of organisms (Gardner 2009) as well as distributions of species in a population were plausible results of the process of natural selection (even if other mechanisms, such as Lamarckian ones, were also used by the first Darwinians).

Selection, unlike divine design, explains adaptation as a fit between organisms and their environment (see below for further explication of this). The diversity of environments in which species find themselves implies a variety of adapted species; therefore, selection explains adaptation through what is called *adaptive radiation*. And finally, the striking similarity of forms between different species of the same genus, or even different genera of the same family, that has been noticed since the eighteenth century by authors like Buffon or Diderot, and then vindicated by, e.g., Geoffroy Saint-Hilaire, and the so-called "transcendental morphologists," is explained by the fact that organisms of different taxa share a common ancestor – a fact that is entailed by the architecture of the tree of life.

However, the rise of Darwinism did not bring about a complete shift in the questions and tools of biology. Rather than wiping out centuries of research in the science of life, Darwinism gave a new and coherent meaning to some accepted facts and descriptions. Instead of rejecting teleology outside science, it provided a way of interpreting teleological phenomena so that they did not depend upon non-naturalistic assumptions, such as hidden intentions on the part of organisms or their creator; it retained the results of traditional taxonomic efforts and conceived of the systematic proximities in the classification of species as historical entities, as Darwin himself noted at the end of *The Origin of Species* (even though, of course, the Darwinian view raised new questions and resulted in new criteria and methods for systematists; cf. Ghiselin 1980).

Thus, evolutionary theory appears to us as the most successful and integrative framework for research strategies in biology generally. Before investigating the details of the philosophical challenges raised by the two Darwinian claims, it is useful to situate the evolutionary approach within the larger endeavor of biology. In this context, Mayr (1961) distinguished between two kinds of causes that can serve as answers to the question *why*. When asked "Why does this bird fly along the seashore to the South?" one can answer by pointing out its physiology, respiratory system, the diverse pressures on its wings, and the streams of air around it: these indicate the *proximate causes* of the bird's flight. But one can also answer by emphasizing that the way the bird chooses to go to the South curiously corresponds to the old demarcation of the continents, implying that the migration trajectory is the result of natural selection acting on this species of bird. This is the *ultimate cause* of the bird's flight towards the South. Notice that the proximate causes concern only *one bird at a time*, and that each bird is affected by them in the same way: they are generic causes. In contrast, the ultimate cause concerns the ancestors of this bird *collectively*, not only the one observed bird. In this respect, the two kinds of causes can be said to correspond to two kinds of biological disciplines. On the one hand, we have the sciences of the proximate causes: molecular biology, cellular biology, genetics, physiology, endocrinology, etc. On the other hand, we have the sciences of the ultimate causes, which are all those disciplines belonging to evolutionary biology: population genetics, quantitative genetics, behavioral ecology, systematics, phylogenetics, paleontology, etc.

Having thus characterized evolutionary theory as a specific set of research programs within biology, and having defined those programs by their use of the hypothesis of natural selection, we can now put evolutionary theory in philosophical focus. This could, in principle, mean two things: either a focus on the philosophical problems raised by evolutionary theory, and on their putative solutions, or alternatively, a focus on philosophical problems that are illuminated by evolutionary theory. It could indeed be argued that the rise of Darwinism has been one of the most significant conceptual shifts in the history of science, and therefore has had tremendous impact on all areas of philosophy. However, most of this chapter will be concerned with the former theme: philosophical problems within the field of evolutionary biology. The last section will briefly sketch a few features of the latter.

Philosophical issues in evolutionary biology can be grouped along two axes: first, in keeping with the distinction between the two main claims of Darwinism, there are issues concerning *patterns* (mostly, patterns captured in the structure of the tree of life) and issues concerning *processes* (mostly, natural selection). Second, philosophical issues may concern, foremost, our way of knowing things, in which case we refer to them as *epistemological* issues; or they may concern the things themselves, as exposed by science, in which case we refer to them as *metaphysical* issues. In the following, we will first address problems related to processes; these will essentially concern the nature and the limits of explanations that rely on natural selection. Some will be more epistemological, while others will be mostly metaphysical. In the second section, we will turn (less extensively) towards some problems regarding patterns; the discussion will be kept brief because many epistemological problems concerning patterns are related to methodological problems concerning proper classification, which are dealt with in other chapters of this book.

Evolutionary Biology: Philosophical Issues Concerning Processes

What is a Selectionist Explanation?

Selection, Population Genetics, and Fitness

Natural selection is a process that is expected to take place in a set of individuals whenever the following requirements are fulfilled: (i) the individuals differ from each other; (ii) the traits that are different are hereditarily transmitted in such a way that the pattern of variation of traits in the new generation is not wholly different from that in the parent generation (e.g., taller parents tend to have tall offspring); (iii) these traits have a causal influence on the reproductive chances of their bearers. After Lewontin (1970) these requirements are often referred to as the condition of variation, the condition of heritability, and the condition of fitness. (It is worth noting that Godfrey-Smith 2009, in describing the various formulations of these conditions, shows that none of these versions can embrace all cases of natural selection.) As a consequence of these conditions, the frequency and the value of heritable traits may vary across generations, until one trait value becomes established in the population, or else an equilibrium between some values is reached. This, then, is evolution by natural selection. It must be kept in mind, as Fisher noted at the outset of his benchmark volume on natural selection (Fisher 1930), that natural selection is not evolution: that is, the changes brought about by natural selection may occur alongside other changes in such a way that in the end no salient change in the population has occurred; conversely, it may happen that evolution occurs, but without natural selection playing a causal role. For example, mere intergenerational random variation (called "drift"; see below) entails evolution.

As they stand, the requirements for natural selection are not restricted to entities – or sets of entities – of a certain type, size, or level of complexity. Anything that meets the requirements is susceptible to the process of natural selection. Thus, researchers have proposed a theory of natural selection of macromolecules, in order to account for the origins of life (Eigen 1983; Maynard-Smith and Szathmary 1995), and – at the other end of the spectrum – theories of natural selection of ideas in order to explain cultural evolution (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Campbell 1990; see section "Evolutionary Psychology"). By the same token, when one meets a set of individuals which fulfill these requirements, one can assume that those individuals have undergone natural selection, and that some of their current properties present its effects.

Population genetics provides models of biological evolution by natural selection. These models often describe a state of equilibrium expected when no selection occurs, called the Hardy-Weinberg (HW) equilibrium, which is derived from

Mendel's Law in populations with sexual reproduction. (Conditions for this equilibrium include infinite populations and random mixing; these are of course idealizations.) The fact of natural selection means that organisms differ in their chances of reproductive success, which implies departures from HW equilibrium. Population genetic models describe evolutionary dynamics as a function of these chances for different genotypes. Models differ according to the way they present intergenerational change (whether generations overlap or not), population structure, etc.; among the most widely used ones are the Fisher-Wright model, the Moran model, and Kimura's stepping-stone model (Ewens 2004). They generally handle gene frequency change at one locus, and sometimes at two loci, but seldom at more than two loci, because otherwise they would become intractable. One way to think about these models is to say that they take natural selection, mutation, migration, and random genetic drift (that is, stochastic fluctuations correlated to the size of the population) as forces acting on the population of genes and move that population away from its equilibrium, exactly as mechanical forces modify a zero-acceleration state that is the equilibrium state of a mechanical system. In this sense population genetics shares epistemic properties with classical mechanics.

Fitnesses (often notated *w*) are the values of differential chances of being represented at the next generation inherent to different organisms, alleles, or genotypes. Natural selection can be seen as "the survival of the fittest," as Darwin wrote in the last editions of the *Origin*, influenced by Spencer (and concerned by the risk of inducing an erroneous sense of agency with the word "selection"). After Fisher and the Modern Synthesis, "fitness" became a crucial technical term, because it entered as a variable into equations of population change. Controversies still rage about its proper interpretation (e.g., Ariew and Lewontin 2004; Bouchard 2011; Abrams 2007; Ramsey 2013; Sober 2001). For our purposes here, suffice it to say that "fitness" involves a mix of survival and fecundity: what counts for evolution is the chance of having heritable traits represented across generations, which in general is a function of the number of offspring, but may also be attested by an organism's chance of survival. In some population genetic models, however, only viability is taken into account, for purposes of simplicity; whereas in some behavioral ecology models, fitness is represented by a proxy, e.g., energy intake. Either way, the logical form of selection remains the same. In most models, fitness is quantified as the number of representatives of a genotype or a trait in the next generation (or the probability distribution of representatives, given that the models are probabilistic). Often traits are not underpinned by one locus, but by a huge number of loci whose effects are small and additive, as is the case for, e.g., height in humans; often, too, they have continuous values. Quantitative genetics is the study of the evolution of continuous traits (such as size) in the absence of knowledge of their genetic makeup (Falconer 1981). It can also predict how phenotypes will evolve, by modeling their value and frequency as a function of the intensity of selection (formalized as a "selection coefficient") and the value of heritability.

Following Orr (2009) it is useful to distinguish between *individual fitness* – that is, the probability distribution of the offspring of an organism, that many philosophers interpret as a propensity, after Mills and Beatty (1979) – and *trait fitness*, which is a “summary statistic” that denotes the probability distribution resulting from the aggregation of the individual fitnesses of all organisms belonging to the same type (for example, having the same trait value for a given trait, or sharing the same allele). Trait fitness is what enters into the equations of population genetics, and allows researchers to predict evolutionary dynamics.

The Modern Synthesis placed population and quantitative genetics at the heart of the investigation of evolution because they provide a mathematical understanding of the process of natural selection. As modeling practices, these sciences simplify reality. In particular, real organisms have very complex genomes, consisting of thousands of genes (which in aren’t even necessarily physically discrete or continuous units), whereas population genetics models typically model only one locus, or at most two. However, given that each locus occurs against a huge variety of genetic backgrounds, the reasonable assumption is that all the effects that different genetic backgrounds – that is, interaction with other genes within the organism – will have on the phenotypes (and thus reproductive chances) of the alleles for this locus will cancel out. Indeed, population genetic one- or two-locus models do correctly represent and predict the evolution of traits in a given population of organisms (Gillespie 2004), as has been demonstrated many times since the 1930s.

On the basis of this general understanding of evolution, the proponents of the Modern Synthesis made several assumptions that have recently came under criticism, in the light of certain empirical findings. First, they equated inheritance with genes, and variation with recombination and mutation, which was recently challenged by empirical evidence for non-genetic forms of inheritance (Jablonka and Raz 2009). Second, they assumed that development – that is, the process through which a zygote goes from conception to adult or reproductive stage – does not matter to evolution, since what counts evolutionarily are the chances of reproduction of a phenotype. The recent research program of “evo-devo” aims to reintroduce development into evolutionary biology by arguing that differences in development result in important differences in evolution (Raff 1996; Hall 2003). In regards to variation as well, population genetic models make important assumptions that have at times been questioned. Obviously, if variation, for generation after generation, were to focus on the variants that are best adapted to the environment, selection would be superfluous (that is, even without selection the course of variation would lead to the fittest phenotypes). Modern Synthesis theory held that variation, consisting of mutation and recombination, is therefore “random,” in the sense that it is decoupled from the state of the environment – which, empirically, is usually the case. Yet claims that variation is actually not random have arisen on a regular basis since the Modern Synthesis took shape, including the recent revival of “Lamarckism” (though it is not properly called Lamarckism, see Merlin 2010) advocated by Jablonka and Lamb (2005). Indeed, the existence of *some* instances of non-random and beneficial variation need not be a threat to the validity of natural selection in general (Huneman 2014b).

In this picture, each of the three conditions of natural selection exerts an effect on evolution: the more random the *variation*, the more room there is for selection; the greater the differences in *fitness* or selection coefficient, the faster does evolution proceed (fixation of high fitness traits); and of course, a greater degree of *heritability*, for a given selection coefficient, also increases the rate of evolution. Heritability can metaphorically be viewed as the strength of a "memory" that, generation after generation, retains the results of natural selection: if it is very weak, it will be difficult for selection to bring about the highest fitness variants.

Finally, a fourth important variable is the *population size*. For a fixed level of heritability and a fixed selection coefficient (or fitnesses), the size of the population may change the outcome of the evolutionary dynamics, since in small populations stochastic fluctuations are large and may prevent the highest-fitness variants from reaching fixation, that is, having a frequency of 100 % in the population. When population geneticists speak of "random genetic drift," they refer to these stochastic fluctuations, especially emphasized by Sewall Wright (Wright 1932). The content of this concept is still controversial. Biologists have vacillated between seeing drift as a deviant outcome (deviant from what is expected based on fitness values) and as a proper cause of a proper outcome in their models (especially in gamete sampling) (Plutynski 2007). When fitnesses differ, drift and selection drive evolution, but the conceptual interpretation of their combination is problematic, since drift is not a force independent of selection but a stochastic fluctuation occurring during the selection process (see section "Metaphysics of Selection: Causation" below). By contrast, when fitnesses are equal, drift alone drives population changes, and diffusion models can be used to represent such dynamics.

The overall relevance of drift in actual evolution depends upon what the most common population sizes are. In any case, when alleles do not harbor fitness differences, drift may drive some of them to extinction. Kimura used this insight as the basis of his *neutralist theory* of molecular evolution, which argues that large parts of the genome in many species have been shaped by neutral evolution, rather than natural selection (Kimura 1983). The relative amount of neutral evolution has been an important topic of controversy in population genetics since the 1980s (Gillespie 2004), when the huge importance of neutral evolution was first acknowledged; since then, there has been progressively more evidence of "positive selection" (Voight et al. 2006), (i.e., the process by which new advantageous genetic variants sweep a population).

Properties of Selectionist Explanations

Three general features of selectionist explanations should be noted. First, they belong to what Mayr (1959b) called "population thinking"; that is, selection is always understood to apply to a collection of entities, since only *differences* in relative fitness matter. In this respect, explanation by selection might be contrasted with what Sober (1984) called "developmental explanation," namely, an explanation of a property that appeals to the process through which that property was acquired. The developmental explanation of the composition of a football team refers to the sum of the experiences of each of its players; the selectionist explanation refers to the choice of the team by the manager, who set a criterion of competence and then evaluated all available football players by this criterion. What is characteristic for selectionist explanations as instances of population-level thinking is the fact that there are no specified criteria of admission other than reproductive success.

In this view, population genetics appears analogous to statistical mechanics – the science of ensembles of gas molecules, which defines state variables that allow physicists to model coarse-grained descriptions and make predictions for an ensemble's collective evolution. Fisher (1930) proposed such analogy, comparing the mean fitness of populations to the property of entropy.

A second important feature is that two traits can be correlated, either for morphological or for genetic reasons; an illustrative example of this is pleiotropy. The two correlated traits will always be selected together, and the two types of individuals they define will have the same fitness. Elliott Sober (1984) coined the terms "selection-for" and "selection-of" to distinguish between traits that are indeed the targets of natural selection, since their ecological consequences increase reproductive success, and traits that are selected because they are correlated to the former. Conceptually, this distinction involves an appeal to what philosophers call "counterfactual thinking": when there is selection of a trait A, but only as by-product of selection for another trait B, it means that if organisms had A without having B, A would not have increased in frequency. However, population genetics has designed methods to distinguish between selected and correlated traits (Lande and Arnold 1983).

A third important feature is that population and quantitative genetics use fitness values as variables associated with traits and alleles, but do not model the *causes* of fitness values. The latter goal is exogenous to population genetics, since what determines the fitness value of a genotype or a trait is the way it relates to environmental demands. Fitness values only record differential performances of types of individuals (types being defined by shared traits of interest) in the environment.

When applied to extant species, population and quantitative genetic models can identify which traits are expressed (or will go to fixation) due to natural selection just by assessing the fitness values of traits – even without considering the problems associated with estimations of fitness in nature – but they don't offer any explanation of *why* natural selection is taking place. Instead, the causes of fitness or selection are a subject of *ecology* (Wade and Kalisz 1990). Ecology was defined by Haeckel, the most famous Darwinian of the late nineteenth century, as the "science of the struggle for life." Ecological interactions such as competition, predation, or mutualism between organisms of various species explain the differential successes of types of organisms, as well as the extinction and succession of species in a community or an ecosystem.

Ecology studies the causes of fitness, with the fitness values being the variables through which population and quantitative genetics capture evolutionary change. Therefore, evolution by natural selection is the subject of two distinct sciences: population/quantitative genetics and ecology. The latter tries to understand the reasons why natural selection has designed organisms the way they are; in other words, it explains biological traits as adaptations to the environment. For instance, when behavioral ecology studies the mating behavior of gorillas, it asks why strategies such as monogamy or polygamy have emerged in a given species in a specific environment (Dunbar 2001), and then offers answers by demonstrating that one particular strategy optimizes reproductive success in these conditions. (See section "Genes, Dynamics, Optimality, and Strategies" below on optimality.) More generally, several evolutionary disciplines ask why organisms are the way they are, by asking why they have the traits they have. When it comes to species of the past, clearly one should use particular methods because, unlike in behavioral ecology, a straightforward modeling of the parameters is not possible; yet fundamentally, paleontology and behavioral ecology ask the same kinds of functional questions about the presence of traits and the design of organisms.

The conceptual duality of natural selection becomes even more challenging when one considers that ecology is also dual, because it comprises not only the science of ecological interactions affecting individuals, i.e., *behavioral ecology*, but also the science of species interactions, i.e., *community and population ecology*. The latter of course defines the background against which the former takes place (e.g., the behavior of foraging organisms is partly determined by the general competition between species that prey on the same prey). Population genetics models a certain population of a given species, in which alleles are changing because of mutation and migration; in general, the environment is considered to be constant in this. (Sometimes it is variable in time, but nevertheless, its species composition is not part of what the model tries to explain.) In contrast, for community or population ecology the genes are an invariant factor, and the species of interest are what varies.

In sum: the epistemic duality of evolutionary biology – population genetics vs. ecology – makes for a complex structure, which we will explore in more detail below.

Epistemology of Selectionist Explanations

Genes, Dynamics, Optimality, and Strategies

Explanations based on natural selection thus gives rise to two different interpretations. On the one hand, population genetics analyzes the dynamics of alleles or genotypes in a population that contains different fitness values. Natural selection here is a specific feature of the dynamics (i.e., differences in relative fitness); the selectionist explanation therefore shares the epistemological status of a mechanical science. On the other hand, when biologists such as behavioral ecologists investigate, for example, the function of figure-eight-shaped waggle dance of bees, they assume that this behavior is somehow suited to the environment of the bees – in other words, that it is an adaptation. In so doing they assume that the behavior has resulted from natural selection, because it would have been selection that optimized the trait in response to the environment (Mayr 1983; Maynard-Smith 1984). Natural selection here is thus seen as an *optimizing process*: by constantly retaining high-fitness variants it maximizes fitness, and fitness maxima correspond to optimal traits. (When the traits have a fitness value that is frequency dependent, we do not see optima but strategies that are such that when they are generalized, no variant strategy can invade the population.) Epistemologically, the status of such knowledge might be said to correspond to economics as a science of behavior based on the principle of maximization of utility. As a matter of fact. behavioral ecology uses evolutionary game theory (Maynard-Smith 1982), which is mostly an extension of economic game theory – one where the payoffs of the strategies are not defined in terms of utility but of fitness.

Moreover, the two aspects of natural selection differ with respect to the kinds of objects they deal with. In population genetics, selectionist explanations pertain to the dynamics of *allele* frequencies. In behavioral ecology, it seems that entire *organisms* are what is at stake, since natural selection seems to optimize the traits of organisms in the face of environmental conditions. Notably, in this latter context one often does not know anything about the genetic make-up of the traits of organisms. Within evolutionary biology, intense controversy continues over the levels and units of natural selection: does it target mostly genotypes or phenotypes, mostly alleles or organisms? (See section "Targets and Limits of Selection, 1: Levels of Selection" below.) But regardless of this controversy, the levels at which population genetics and behavioral ecology locate their subject are different: for the latter it is organisms, and for the former, genes.

As "Formal Darwinism" (Grafen 2002, 2007) importantly emphasized, these two takes on natural selection do not always concur. In many cases, maximum fitness will not be reached by natural selection. This is especially true in the case of frequency-dependent selection (Moran 1964), but also in the simple case of heterozygote superiority (where for principled reasons, the heterozygote genotype cannot fix in the population). However, behavioral ecologists generally assume that the gene dynamics will match what an optimizing trend would predict and will therefore support their hypotheses. This is what Grafen (1984) called the "phenotypic gambit" – a bet about the relationship between phenotypes and genotypes. Formal Darwinism has shown that there are indeed isomorphisms between descriptions of evolution in terms of changing allele frequencies and descriptions in terms of optimization of organismal traits, so that the phenotypic gambit can be the default position. This formally justifies the intuition behind many proposals in behavioral ecology. Philosophically speaking, it justifies a unification of the two approaches to evolution, as the result of which it is understood as both the object of a kind of mechanics and that of a kind of economics (Huneman 2014a, c).

Epistemology of Selectionist Explanations: Analyticity and Historicity

Analyticity

Population and quantitative genetics is mostly couched in the mathematical language of statistics. In this context, many authors have tried to provide very general formulations of evolution by natural selection. Fisher first forged what he called the "fundamental theorem of natural selection" (FTNS), which states that intergenerational change in the mean fitness of a population equals the additive genetic variance, hence is always positive (i.e., fitness always increases). He saw this as an analytic truth, a priori established, whose status equals the status of the second principle of thermodynamics (for Fisher, both population genetics and thermodynamics were sciences of macroscopic variables defined on the basis of collectives).

Fisher's theorem was controversial, since many authors opposed it on the grounds that population genetics, as indicated, does not always predict fitness maximization. Recent interpretations of the FTNS highlight that the quantity referred to by the theorem is not a global change in mean fitness but, more narrowly, a mean fitness change directly due to natural selection (Ewens 1989; Frank and Slatkin 1992; Edwards 1994). To this extent, the theorem can be made to accommodate empirical cases where mean fitness decreases; in these cases, negative changes in mean fitness due to what Fisher called "environmental deterioration" (a term whose interpretation is debatable) overwhelmed the positive effect of selection.

In any case, the parallels that Fisher drew to statistical mechanics have been seriously considered by several authors, who tried to develop population genetics in a way rigorously analogous to statistical mechanics, viewing the construct of fitness as formally analogous to a kind of entropy (Barton and Coe 2009).

But other general abstract formulations have been proposed as well. George Price suggested that evolutionary change can be captured in a simple quantitative genetics formula that can be analytically derived (Price 1970):

$$\Delta z = \mathrm{Cov}(w_i, z_i)/w + E(w_i \Delta z_i)/w$$

where z (resp. w) is the mean trait value (resp. mean fitness), w_i is the fitness of individuals i, z_i their value of the trait, and Δz_i the change of this value between individual and offspring. This so-called "Price equation" decomposes evolutionary change into the effect of natural selection (captured as covariance between fitnesses and traits) and the transmission biases (the expectation term) (Gardner 2008).

Interestingly, Fisher's FTNS can be derived from the Price equation if "fitness" is taken as the focal trait. But it should be made clear that the variable z, whose change is modeled by the equation, can also mean other properties, such as the frequency of alleles – hence the Price equation is even more general than the principles of quantitative genetics. Moreover, the Price equation, being mathematically true, is a *description* of evolutionary change, but cannot in itself provide *causal* information on evolutionary processes. Grafen's Formal Darwinism (see above) construes its isomorphism between population genetics and optimization on the basis of the Price equation. Other general formulations of evolution have been proposed, some of them in the context of what is called "replicator dynamics," others in the context of "adaptive dynamics" (Metz 2008).

The above discussion of the analytical or formal side of evolutionary theory gives rise to an occasion to mention the so-called *tautology problem*. If natural selection is defined as "survival of the fittest," one could object to Darwin that in the absence of other evidence regarding the capacities of organisms, the "fittest" are precisely those who survive, so the main principle of the theory constitutes a tautology. One response to this is that there are other, independent pieces of evidence for fitness (drawing on physiology, ecology, etc.), or that there are cases where the fittest do not overcome all others evolutionarily (i.e., in the case of drift), demonstrating that the statement is not analytical. But another plausible response consists in accepting the criticisms, and saying that current evolutionary theory has at its core a mathematical theory – mathematics being a system of analytical judgments. This concession does not therefore give up on the scientific validity of the theory (no more so than acknowledging the mathematical nature of modern physics would diminish the validity of physics).

Historical Understanding

As Bock and von Wahlert (1963) wrote, we must distinguish the *processes* of evolution, which involve – but are not to be equated with – natural selection, and the *outcome* of evolution, namely phylogenies and the phylogenetic tree. However, no actual process of evolution could be understood solely through theoretical knowledge of evolutionary mechanisms, in the absence of historical data. For instance, many terrestrial vertebrates are tetrapods: one could imagine a selectionist hypothesis concerning the adaptive origins of their four limbs, since this configuration is obviously adaptive for locomotion. However, there is another reason for those four limbs: marine ancestors of those vertebrates had four fins, so the four limbs are a legacy, resulting from what we might call "phylogenetic inertia." The point is that natural selection often explains the appearance of such traits, but not their appearance in a particular clade. The selectionist explanation has to be historically situated in order to determine what the correct *explanandum* is – the one for which natural selection would be the right *explanans*. Thus, no explanation of the presence of characteristics in the members of a given population or species is available through the sole application of population genetic models of natural selection. The distinctive characteristic of evolutionary theory, if we assume that its explanatory strategies are always related to some use of the selectionist explanation, is that it brings together certain formal models, written in mathematical language in the modality of pure necessity, and certain historical narratives (Gayon 1993; see Richards (1992a) for an argument in favor of evolution as a narrative).

Thus, evolutionary biology is indissolubly both a formal science, to the extent that evolutionary change can be captured through analytic formulae and models, and a historical science, as soon as it comes to understanding actual past and present evolution at any scale. This latter methodological aspect also implies that few empirical inquiries in evolution can be made without *comparative data* (Endler 1986), in order to avoid incorrect, a historical invocation of natural selection mechanisms – such as in the tetrapod example above. Often a divergence of results between studies can be traced back to differences between the sets of comparative data used by the researchers (Sober and Orzack 1994, 2001; Griffiths and Sterelny 1999, pp. 240–250).

This pervasive element of historical narrative in neo-Darwinism accounts for the historical meaning of all biological terms in evolutionary theory. Taxonomies are obviously and easily reinterpreted by history. The concept of homology - initially defined by Owen (1843) as the same organ in different animals under every variety of form and function - that helps systematists build their classifications acquires in the light of evolutionary theory the historical status of “signs of common descent,” as for instance in the case of birds’ and bats’ wings. (See chapter “▶ Homology: A Philosophical and Biological Perspective,” Vol. 1.) Homoplasy, as the other kind of similarity across species, seems less of a historically significant concept at first glance: similar selective pressures gave rise to similar devices, representing similar adaptations to these pressures. But is it really the case that the concept of adaptation lacks any historical dimension?

The question of whether adaptation is a historical concept is widely debated. Philosophers (Burian 1983; Sober 1984; Ruse 1986; Griffiths 1996) concede that “adaptation ascriptions are causal-historical statements” (Brandon 1996), since to say that a trait is an adaptation is to say that it has somehow been selected for some of the advantages it gave to its bearer via differential reproduction. (Note that “adaptation” is a property of *traits*, whereas in a pre-Darwinian context, and often in non-evolutionary biology, “to be adapted” and “adaptation” are features of *organisms*; though many evolutionists as well often use “adaptedness” to refer to this latter kind of adaptation.) It remains to be decided whether this sums up the full meaning of the concept – given that biologists often do not appeal to historical facts in order to describe adaptations, but just forge optimality models with current data, as done in behavioral ecology. Reeve and Sherman (1993, 2001) advanced a powerful “currentist concept” of adaptation, as opposed to the historical concept: “An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment” (1993, p. 9). Having distinguished two goals of evolutionary research – the first being the explanation of the *maintenance* of traits, and the second the reconstitution of a *history* of lineages – they argue that the former essentially needs the currentist concept, whereas the latter is much more closely related to the historical concept. Notwithstanding one’s view on this matter, the fact that there can be a historical component to adaptation ascriptions is important, since it allows biologists to distinguish between the origin of a trait as an adaptation and its current presence and maintenance. A trait that is adaptive might not have emerged as an adaptation, or might have emerged as an adaptation for some other use. This is captured by the concept of “exaptation,” suggested by Gould and Vrba (1982); an example would be insect wings, which probably emerged as thermoregulatory devices (Kingsolver and Koehl 1989). Exaptation has proved to be a useful concept for our understanding of a lot of features that appeared during the evolution of hominids (Tattersall 1998).

However, one should not conflate the two meanings of the historical characterization of adaptation: there is a *definitional* meaning and an *explanatory* meaning. On the one hand, selection *defines* adaptation, since a trait being an adaptation means that it originated through natural selection. But on the other hand, we say that selection *explains* adaptation; this is not contradictory to the definitional meaning, because we now mean that the explanation of a given adaptation may refer to concrete selective pressures in the given environment, which provides an agenda for the experimental testing of hypotheses. An example of such experiments, and of the explanatory use of the historical concept of adaptation in their interpretation, is a study on the differential sensibility of plants to gradients of metal in soils (Antonovics et al. 1971).

Metaphysics of Selectionist Explanations

Laws in Evolutionary Biology

The hybrid epistemic status of evolutionary biology inclined philosophers to enquire about the status of laws in this discipline. Some of them argued that there are no laws in evolutionary biology (Beatty 1997; Rosenberg 2001; Brandon 1997 vs. Sober 1997), or in biology generally (Smart 1959). An analogous controversy occurred among ecologists, with Lawton (1999) doubting that ecological laws exist and other authors (e.g., McGill and Nekola 2010) arguing that ecology does indeed capture specific laws.

Laws of nature are general statements formulated under the modality of necessity. The logical-positivistic account of science viewed explanation as a deductive argument whose conclusion is the *explanans*, and whose premises combine certain laws of nature with particular statements of facts (the so-called “deductive-nomological” account of science; Hempel 1965). Even though the philosophy of science has mostly turned away from positivism since the 1970s, many authors still attribute a crucial explanatory status to laws (e.g., Lange 2009). The usual puzzle in philosophy of science is to find a criterion distinguishing accidental generalities (such as “All mountains are less than 100,000 m high”) from laws (Ayer 1956). As a solution, Dretske (1977) claimed that laws have to be conceived as relationships between “universals” (for instance, the law of gravitation holds between the natural properties mass and distance, which are universals, as opposed to individual bodies, which are particulars). In any case, laws should support counterfactuals; this means that if some variables are changed within them, the results should be affected in a predictable way. The implication is that law-like generalizations can be used in explanations, whereas accidental generalizations seem not to allow such a use, and even less a predictive use.

Yet the very notion of law, as used by biologists, is often ambiguous. Some laws concern the correlation of variables in a given empirical range: for instance, the correlation between body size and latitude (“Bergmann’s rule”); or the species–area relation in ecology. Many laws in paleontology can also be seen as such generalizations: “Dollo’s law” about irreversibility, “Cope’s law,” etc. These laws actually concern patterns, and are mostly established through induction; often they are captured in what physicists call “phenomenological models.” However, one can still wonder why such pattern laws are found, hence investigate the processes supporting them. That then leads to the quest for what scientists often call mechanisms, captured in “mechanistic models.” Philosophers of science would mostly say that the “process laws,” related to the mechanistic model, are the most explanatory and hence have to be called genuine “laws” (whereas they would be content with calling the other laws “rules,” for instance “Bergmann’s rule”).

Many controversies in ecology actually concern these underlying laws. Thus ecologists wonder, for example, whether there is one such underlying law yielding the species–area relationship. Advocates of the absence of laws in ecology argue that given the complexity of ecological systems, there may be many processes accounting for the various patterns of biodiversity we observe, but not a single, overarching mechanistic model likely to capture them all.

Ecology aside, what about other aspects of evolutionary biology? Clearly, in evolutionary theory most generalizations do not seem as robust as typical laws of physics (in fields such as particle physics; though when it comes to cosmology, physics arguably does involve history, and law statements may be traced back to the contingency of primordial history). Most law statements concern species of organisms (e.g., “Bonobos are promiscuous”), and, because of the contingencies of evolution, these species could have been absent or different. They are not “natural kinds” in the metaphysical sense, unlike the chemical elements, of which any chemical substance is made and which can robustyl and a historically be defined in terms of an atomic number - setting aside the complications added by the fact of a cosmological history. Any term in a putative biological law *p* instead seems to be contingent upon the facts of evolution, which makes statement *p* less than a law. As Beatty (1995) argued, Mendelian laws are contingent upon the fact of sexual reproduction, which is a possibly contingent product of evolution on earth. And even the universality of the genetic code is a generalization confined to our planet, where it holds due to the universal descent of life on earth from a contingent fact – a “frozen accident” (Crick 1968); the same correspondence laws between nucleotides and amino acids cannot be expected to hold on other planets. This contingency of generalized propositions affects the whole of the system of supposedly law-like statements in biology.

The only evolutionary statement that could be a law is, thus, the one enunciating the process of natural selection itself, since it specifies no particular entity. And this indeed accounts for the important difference made between pattern laws and process laws. For instance, Bergmann’s rule states a pattern associated with the geographical distribution of clades or species or populations of species: larger ones tend to be found in colder environments (which of course correlate with latitude). This pattern is explained by the fact that larger animals have a lower surface area-to-volume ratio than smaller animals, which implies that they lose less body heat per unit of mass. This, in turn, entails that, the colder the environment in which a species is found, the more likely selection will favor the variants that better resist the cold, which are – everything else being equal – the larger ones. Thus the explanatory core of the process is natural selection: all else being equal, organisms better equipped to face the given environmental conditions (i.e., those having traits that allow them to live longer on average and to produce more offspring) tend to pass on their heritable traits, eventually leading to the dominance of these traits in the species. That adapation-to-temperature process itself could hardly be seen as a law; rather, it is an instance of natural selection. (One would reasonably resist calling a law each case where natural selection yields a specific pattern regarding the distribution of some traits.) It is thus plausible, in our example, that the law underlying Bergmann's rule would be something like "the law of natural selection," a suggestion controversial among philosophers (Bock and von Wahlert 1963; Sober 1984, 1997; Brandon 1996, 1997; Rosenberg 1985, 1995, 2001).

Rosenberg (2001) argued that what Brandon (1996) calls the Principle of Natural Selection (PNS) – briefly summed up as, "When variation is causally connected to differential ability to survive and reproduce, differential reproduction will probably ensue" – is the only law of biology. He relied on Williams' (1970) axiomatization of the theory, which conceives of fitness as an undefined primitive term, e.g., a term for which some definitions, in some contexts, can be given only outside evolutionary theory, in another theory. But, even if by convention we say that the PNS is a law, we still face the question of how it differs from other kinds of law. In effect, unlike physical laws, the PNS does not refer to any natural *kind* of property such as mass, electric charge, etc. The sole property involved in some of its formulations is fitness, which only captures context-dependent consequences of some physical properties evolutionarily relevant in a given setting (for example, the color of moths is a fitness parameter in industrial melanism only because there are predators capable of vision). So the PNS can become the equivalent of a physical law – stated in probabilistic language – only if and when the physical characteristics of the properties contributing to fitness are *specified*, a specification that is always context dependent. For instance, the "optimal shift towards viviparity" in some marine fish described by Williams (1966) results from a kind of rule, since he states the parameters ruling the selection pressures (density of predators, physiological cost of reproduction); these parameters in turn determine a range of relevant physical properties for selection. In this case the PNS becomes predictive, and we can test it by building experiments in which the values of the proper variables vary.

The PNS aside, there surely are a number of genuine laws in evolutionary theory; however, those kinds of propositions are not so much empirical laws as *mathematical laws*. In a way, evolution contains both statements modally stronger than physical laws (since they are purely mathematical statements) and statements nomothetically weaker, such as those derived from the PNS through its empirical instantiation. Rather than being a law, the PNS ultimately proves to be an *explanatory schema*, providing ways of explaining and building models through its more or less empirical instantiations. The least empirically instantiated models are the models of population genetics; the most empirically instantiated are rule-like generalizations, such as paleontological ones.

Metaphysics of Selection: Causation

Philosophers of science have moved away from logical positivism and Carl Hempel's claim that explanation consists in subsuming phenomena under laws. Instead, the view has been on the rise that genuine explanation must be causal – under one of various possible conceptions of causation (probabilistic, physical, counterfactual, Humean, etc.; Tooley and Sosa 1983). Hence, notwithstanding the controversy over the existence and nature of laws in evolutionary biology generally, and over the status as law of the PNS in particular, philosophers are expected now to consider the causal role of selection. Two simple (and related) issues arise: What does natural selection causally explain? And, is it even a cause (vs. some other kind of explanation)?

Attempts to answer the first question generally take one of two views. In the first, selection is a negative, attenuating force: it merely selects, and thus sorts high-fitness traits out from low-fitness ones. In the second view, by contrast, selection assumes a more positive role by being itself *creative*. Thus Mayr (1965) already claimed that selection is not a "purely negative force," since it gradually improves existing traits. Among biologists, this positive view has been widely held: Dobzhansky, Simpson, and Gould shared it. "Creativity" was an important notion for the architects of the Modern Synthesis, since it enabled them to distinguish their view from Mendelian saltationism, which attributed the main evolutionary force to mutation and variation: if selection is creative, then one cannot locate the main reason for evolution at the level of variation (mutations).

In the last decade the debate on the negative vs. positive role of selection has surfaced once more in the field of philosophy of biology. The basic question underlying this ongoing controversy is: what does selection actually explain? It does explain, at a population level, why a trait, *once it had arisen*, pervaded and persisted in a population (1). But is that all? Does selection not, ever, explain why a given individual displays a particular trait? (2) (Should that latter explanation always be given just in terms of developmental effects?) Sober (1984) for one subscribes to the negative view that selection is strictly a population-level explanation, so that the question "Why is trait A present in individual B?" does not fall into its domain.

Neander (1995) challenges this view, in line with Mayr's intuition. Apart from the two questions distinguished above (questions (1) and (2)), there is, according to her, the "creative question," which is: "Why did the genetic and developmental devices underpinning a given trait arise in a population?" Neander contends that natural selection contributes an answer to this creative question, for the following general reason: even if the genotype conditioning a new trait is not created by selection, selection does increase the probability of occurrence of the many alleles composing this genotype.

In a population of diploid organisms, suppose a pool of genotypes of nine loci, and suppose that the genotype G_1-. . .-G_9 has a higher fitness than all the genotypes comprising other alleles G'_i $(1 < i < 9)$, G''_i, G'''_i, etc. Due to selection, organisms with genotype G_1-G_2-. . .-G_9 will have more offspring in subsequent generations than if there had been no selection. Hence, because of selection, the probability that a genotype randomly picked in the next generations comprises one or several G_i will be higher than what it would be without selection (since, without selection, the genotype G_1-. . .-G_9 would have less offspring, thus the alleles G_1, . . . G_9 would be less frequent, and less likely to enter into frequent recombination with other genes into new genotypes). Selection for genotype G_1-. . .-G_9 increases the chances that alleles G_i will be available for variation in subsequent generations, hence genotypic variation at a later generation is different than what it would have been, had there not been genotypic fitness differences (in other words, selection for G_1-. . .-G_9). The thrust of the argument is that genotypic variation at a given stage (i.e., the distribution of genotypes) is not independent from natural selection at an earlier stage, even if allelic variation (as mutation) is not influenced by selection. Hence the claim that only mutation creates the variants (as a sum of mutations) and selection just sorts them is false. To the contrary, *cumulative* selection causally contributes to the appearance (and not only the spread) of traits that are adaptations – assuming that "causation" is broadly understood as a raising of probability or as counterfactual dependence, and not as a mere physical process, as Salmon and other philosophers would have it.

This defense of the positive view of selection can be extended. It has been shown in certain bacteria exposed to stress that selection can increase the mutation rate, providing an advantage in terms of the range of available responses to environmental shifts (Taddei et al. 1995). The notion that the rate of mutation is somehow controlled by selection, while at the same time mutations are the material acted upon by selection, demonstrates a kind of reflexive effect of natural selection on its own parameters. This reflexive structure allows one to say that the traits selected are themselves dependent upon the form of selection pressures, hence are not just sorted but somehow *shaped* by selection. In the case of the stress-exposed bacteria, even if the exact nature of the mutations is prior to selection – that is, not influenced by it – any individual mutation is still counterfactually dependent on selection, since the probability of *its occurrence* is directly dependent on the mutation rate. In conclusion, then, it seems difficult to separate positive causes of the emerging new individual phenotypes ("shaping") from negative causes affecting their spread or extinction ("sorting"). The positive view of selection is likely to prevail.

The second issue that has been hotly debated during this last decade simultaneously concerns the causal status of natural selection and the nature of the relationship between selection and drift: namely, are the latter competing hypotheses? The classical view, stated above, takes drift and selection as two kinds of forces acting (together with the forces of mutation and migration) on an equilibrium model formulated by the HW law. If equilibrium is disturbed, then selection may be at work; and when the fitter allele is not fixed, then random drift must have perturbed selection. Outcomes are the result of the addition of selection and drift, analogously to the summation of forces in Newtonian mechanics. However, this model has been challenged in several papers by Walsh, Ariew, Lewens, and Matthen (Matthen and Ariew 2002, 2009; Walsh et al. 2002; Walsh 2007, 2010). Somewhat deflatingly, these authors claim that selection, migration, mutation, and drift are all not causes, but merely statistical relations resulting from the aggregation of genuine causal processes at the level of single organisms. In population genetic models, these relations are modeled accordingly. These "statisticalists" argue that the individual interactions of the organisms in a population, taken together, in aggregate constitute natural selection; they reject the idea that selection is an additional, exogenous force. Indeed, once all individual-level interactions are specified, all changes in population frequency can be derived: "selection" and "fitness" are just statistical concepts used to describe these population-level changes. Trait fitness is predictive for population genetics, but it is a summation of the fitnesses of many individuals sharing the respective trait and, as a statistical construct, is causally inert.

It has also been claimed by statisticalists that not only is it often difficult to distinguish between selection and drift (Beatty 1994), and not even that drift – far from being another independent process like selection – is something like an error term representing stochastic fluctuations in a directional process that constitutes selection (Brandon and Ramsey 2006) but that fundamentally natural selection and drift are indistinguishably aggregated effects of interactions, so that it is impossible to tell them apart.

Many responses have been elaborated by philosophers. These have ranged from defending selection as a population-level cause (Millstein 2006), to emphasizing the role of individual ecological fitness (Bouchard and Rosenberg 2004), to invoking the causal nature of selection and drift as two variables that can be manipulated through simple intervention (Riesman and Forber 2005), to arguing that even if selection is not another process, the statistical relations at issue can also be expressed by a counterfactual statement of dependence between traits and their frequency change, which amounts to a causal statement (Huneman 2012, 2013). This debate may seem no more than the lofty concern of metaphysicians, but it does have important consequences, as explicated by Walsh (2003, 2013): if natural selection is not a causal explanation, of adaptation the causal explanations must be sought elsewhere, namely, at the level of developmental processes such as organismal activities or physical self-organisation processes.

In general terms, this echoes the way Müller and Pigliucci (2011) present the above-mentioned call for an "extended synthesis" superseding the Modern Synthesis. In the introduction of their volume, they explain that Darwin and the Modern Synthesis biologists did not have any understanding of the mechanisms of variation; whereas we, thanks to molecular biology, are more and more aware of these mechanisms. Lacking a take on the real mechanisms, the Modern Synthesis authors had to model processes in terms of statistics. This explains why population genetics was, for them, at the heart of evolutionary science. But given that we can now grasp the mechanisms of variation directly, we no longer have to ground our evolutionary science on the statistical models of population genetics. Such contrast between "statistical" and "mechanical" understanding is backed up by the statisticalist understanding of selectionist explanations, which sees these explanations as purely statistical and non-causal: hence this view leaves room for other explanations – room to be filled by evo-devo-style explanations, which focus on the inner mechanisms of variation. Inversely, if one is not committed to statisticalism, one may choose to resist Pigliucci and Müller's claim that contemporary evolutionary science should turn to mechanicism and dismiss the Modern Synthesis picture, said by them to be centered on statistics and unable to capture the real causes. We see here how a vivid scientific controversy can hinge on metaphysical issues that revolve around the concepts of causation, explanation, and probability.

Targets and Limits of Selection, 1: Levels of Selection

The PNS is a formal explanatory sketch, but the precise characterization of the process of selection and the entities it involves – the issue of the levels or units of selection – has been one of the hottest controversies in evolutionary biology and philosophy of biology for several decades.

Genic Selectionism

After having studied the collective foraging habits of herds of animals, and found that it appeared as if each animal restricted its own consumption so that resources remained available for subsequent generations, ecologist Wynne-Edwards (1962) claimed that natural selection acts in favor of groups or populations. This claim seemed to contradict the fact that it is individuals who are the entities subsisting and spreading through selection. Against him, Williams (1966) gave a forceful defense of selection – and hence adaptation – applying exclusively to individuals. Since the determinants of heritable variations that are being selected are genes, he concluded that selection acts primarily at the level of the genes. It is worth noting, however, that Williams did not refute the logical possibility of adapted groups, subject to group selection. He merely proved that the examples which had been brought forward as alleged cases of group selection could also be explained by natural selection at the level of genes – the theoretically more parsimonious approach. Along similar lines, Dawkins (1976, 1982) elaborated his view of genic selectionism (the "gene's eye view" of evolution), trying to account for all manifestations of selection. One must distinguish here between genic *selectionism*, which is an assertion about processes of selection, and genic *determinism*, which claims that all phenotypic traits are wholly caused by genes, with no effect of environment or learning. One could perfectly well subscribe to genic selectionism without genic determinism, as did Dawkins himself, as well as Rosenberg (1985) or Dennett (1995). Genic determinism is about development, whereas genic selection is about evolution; the former (which is a straw position now unanimously rejected) claims that the genotype in itself largely controls the construction of an individual's phenotype, whereas the latter takes as central fact that only *differences* in genes matter for the evolutionary dynamics in a population. Thus the genic selectionist concept of a gene only requires that the presence of a gene in a certain environment make a fitness difference, relative to its absence. Commitment to this weaker requisite that genes be "difference makers" (Sterelny and Kitcher 1988) need not be accompanied by any assumption about what it is that genes determine, and through which mechanisms. The genic selectionist view can easily accommodate the massively documented fact that most traits – like human height – are based on a huge number of loci, and that the effects of most alleles vary as a function of environmental parameters (that is, the idea of a "norm of reaction"). Genic selectionism does not rule out the possibility that environment might be as much a determinant in the development of a trait as genes are (Gray 2001).

Hamilton (1963) has been immensely influential in this debate by showing that many apparently altruistic behaviors, i.e., behaviors that are costly (in fitness) for the organism itself, and beneficial for other organisms – such as the sterility of many hymenopteran insects – can be understood at the genic level; this is where the notion of "kin selection" arose (West et al. 2010). At first glance, such behaviors appear rather contradictory to natural selection as a means of enhancing the individual's fitness; hence Wynne-Edwards' appeal to group selection. From a kin selection perspective, altruism has been selected because, although it decreases the fitness of the altruistic individual, it increases the representation of that individual's genes in the next generation, provided that the individual is related closely enough genetically to individuals benefiting from this altruism. This is the case in insect societies, since due to their reproductive structure they are essentially societies of cousins. For example, worker bees are closer to their sisters and queen than to their own putative offspring. Biologists expressed this in a simple rule, "Hamilton's rule," stating that a behavior – or more generally a trait – evolves if and only if $b < cr$, where c is the cost for a given individual, b is the benefit to other(s), and r stands for "relatedness"; the latter is a measure of genic proximity that is often given by kinship relations, but which more generally is rather sophisticated variable, likely to be interpreted in various mathematical ways (Frank 2006; West et al. 2010).

Genic selectionism thus is the claim that natural selection targets the level of the genes; it uses the pervasiveness of kin selection as a key piece of evidence. It has been challenged in several ways by (among others) Gould, Lewontin, Sober, and Brandon. One critical argument is that selection acts only on phenotypes, hence is blind to genotypes. Therefore, the argument goes, the level of genes cannot be relevant for understanding selection. Many genotypes, and therefore many genes, are identical with respect to natural selection, provided that they are genes "for" the same phenotypic trait. Drawing on a notion elaborated by Reichenbach and Salmon in a philosophical debate about probabilities, the argument states that phenotypic interactions *screen off* the efficiency of genotypes and their relationships with the environment. (One says that "A screens off B as a cause of C" if and only if $\Pr(C/A\&B) = \Pr(C/A) \neq \Pr(C/B)$.) It does not deny that genotypes, together with environments, cause phenotypes. Rather, it asserts that this kind of causation does not explain the outcome of selection, since it is both necessary and sufficient for the purpose of explanation to consider the effects of the interaction of the phenotype with its biotic and abiotic environments. The other line of defense, stated by Sober and Lewontin (1982), relies on a *context sensitivity principle* which claims that, since the phenotypic effects of a gene depend on the environmental and *genetic* context of its expression, a single allele cannot be the bearer of the selective causal process. By way of example, the authors cite the case of heterozygote superiority, where it is the diploid genotype (e.g., *AA* or *Aa* or *aa*), and not the single allele (*A* or *a*), that is the genuine entity supporting the selection process (in a classic example of this, only the combination *Aa* confers malaria resistance unaccompanied by sickle cell anemia). It is certainly possible to describe mathematically what happens to a single allele, but this gene's eye view account is not *causally* explanatory, since the real cause resides at the level of the genotype.

Selection: General Formulation and Level-Pluralism

Although biological evolution has been theoretically defined as a change in gene frequencies, the fact that the general model of the process of selection is not committed to any determination of the entities undergoing natural selection implies that these are not necessarily "genes." Thus David Hull (1980) gave a formulation in terms of *replicators* – reproducing entities – and *interactors* – entities whose causal relationships affect the hereditary success of the replicators they are associated with. Selection on this approach is the differential replication of replicators as a function of the interactions of interactors. (It was Dawkins (1976) who first coined the term "replicators," but he opposed it to "vehicles.") In most classic cases of natural selection, the replicators are genes and the interactors are organisms. The gene's eye view claims that genes are the units of selection because they are always the replicators. But of course the formal definitions could be applied to different situations: ones in which replicators could be species or clades, or interactors could be genes themselves or groups. One point of interest of Hull's formulation is that it can handle selection even outside biology – for instance, when we talk about cultural entities. This formal characterization thus offers a more flexible approach to various selection phenomena. For example, in the case of meiotic drive or segregation distorters (cases important to Dawkins' argument) genes are not only the replicators but also the interactors, justifying reference to "genic selection" (Burt and Trivers 2006) – to be distinguished from the stance of *genic selectionism*, which as noted states that *any* selection is in principle taking place at the level of genes.

Concerning genic selectionism, two strong, opposing positions have been put forward among philosophers of biology. The first one, formulated by Brandon (1988), is pluralism: it states that there are several levels of selection (as interactors) and several units of selection (as replicators). On this view it is an open empirical question, in any given case, which are the actual forms of natural selection, although most commonly empirical evidence favors selection at the level of organisms, added to selection at the level of genes and in some cases at the level of groups. The opposite position is defended by Sterelny and Kitcher (1988), who claim that there is always genic-level selection, even if it can often be legitimately captured as a selection process at another level, organismic or supraorganismic. This is so, according to them, even if we cannot have empirical access to this level, and even if it is pragmatically more interesting for biologists to recognize supraorganismic selection processes and treat them as such. The genic level is said to be always the "maximally informative" one.

Those philosophical considerations do not, in fact, impinge on biological investigations. It seems that in practice, biologists are mostly pluralist on this issue (e.g., Williams 1992). However, it is not clear whether the choice between the two contrasting positions could be settled through empirical inquiry alone.

New Group Selection, Kin Selection, and Pluralism

D. S. Wilson and Sober provided new theoretical grounds for the use of group selection (Sober 1988a; Wilson 1992; Sober and Wilson 1994, 1998), postulating what Wilson called "new group selection." Their argument relies on distinguishing and comparing within-group and between-group selection processes. For instance, if "altruism" and "selfishness" are the two traits under focus, selfish individuals do better than altruistic ones in a given group, but the groups that have more altruists generally do better than those that include more selfish individuals (think, for example, of "altruists" as individuals that forage for more resources for the group). The overall number of altruists may therefore increase, if one considers all groups jointly. One consequence is that even kin selection appears as a form of group selection (where the relevant groups are defined by kinship), rather than being genic selection's underpinning of an apparently altruistic phenomenon.

The essence of such approach consists in viewing selection as composed of two selective processes: one at the level of the group, and the other within the group, at the level of individuals (Okasha 2006). Damuth and Heisler (1988) made a useful distinction regarding the concept of multilevel selection, between what they call Multi-Level Selection 1 (MLS1), where the fitness of groups is measured by the number of individuals they comprise in the next generation, and MLS2, where it is measured by the number of daughter groups they can produce at the next generation. The altruism of vervet monkeys warning others about the presence of a predator is an instance of MLS1, whereas species selection pertains to MLS2 (it concerns the greater or lesser ability of a species to speciate).

In the spirit of this multilevel approach, Michod (1999) elaborated a schema accounting for the progressive emergence of new kinds of *units of individuality and fitness*: macromolecules, genes, cells, multicellular organisms, etc. The model relies widely on trade-offs between decreases in fitness at lower levels (for example, the association of individuals creating a common interest, in a way that works against the interest of the individual) and increases in fitness at higher levels (for example, the level of the association itself); this type of trade-off is an exemplary case of multilevel selection. The recurrent problem is, then, to show how, in each case, the tendency for the individual to defect (e.g., by breaking the association), which is an option whenever there is a "common good" (Leigh 1999), can be overcome through this multilevel selection. Michod's approach ignited an important revival of the question of the nature of biological individuality (Bouchard and Huneman 2013), as well as the concept of "organism" – and whether one should accept the existence of "superorganisms" such as ant colonies, or rather talk of degrees of organismality (e.g., Strassmann and Queller 2007).

However, recent developments have shown, first, that kin selection is a very powerful theoretical tool for understanding a great many behaviors and traits, and second, that there are formal equivalences between multilevel selection and kin selection (Kerr and Godfrey-Smith 2002). Moreover, "kin selection" may be understood in a very broad way, where relatedness is not limited to kinship. It then covers many cases where altruistic traits evolve even in the absence of kin groups (West et al. 2007). Kin selection and MLS appear to be two equivalent ways of partitioning the causally relevant factors in a dynamic of evolution: either one defines the various competing *groups* and then expresses selection as the net effect (on the trait under discussion) of intra-group and inter-group competition, or one focuses on the value of *relatedness* and then expresses fitness as the sum of direct (=affecting the relevant individual itself) and indirect (=affecting related individuals, in proportion to their relatedness) fitness benefits (Huneman 2014b) – a measure called *inclusive fitness*. Explanatory pluralism would then consist in allowing for these two approaches to coexist, whereas monism would represent the claim that only one of them really captures the fundamental causal facts. An important argument in favor of kin selection is the empirical fact that it is more widely used than the alternative approach, often because it is more mathematically tractable.

From this perspective, one could argue that inclusive fitness is the most general concept of evolutionary theory, and that evolutionary change can be understood to be directed by maximization of inclusive fitness. This would generalize Fisher's Fundamental Theorem (about natural selection increasing mean fitness) to a yet wider set of cases, including strategic interactions (for which Fisher's Theorem seemed initially problematic; see section "Epistemology of Selectionist Explanations: Analyticity and Historicity" above).

The controversy summarized above bears important consequences for the general scope of the theory of evolution. What is at stake in the discussion of altruism is the possibility of extending selectionist explanations to certain central social phenomena in humans. (See chapters "▶ Great Ape Social Systems" and "▶ Cooperation, Coalition, Alliances," Vol. 2.) If altruism can be explained via kin selection theory, or via Trivers' reciprocal altruism (Trivers 1971) – which holds for populations of nonrelated organisms and is now derived from game theory, particularly from the results of a study of Prisoners' Dilemma by Axelrod (1980) – then the issue of levels of selection entails the issue of the potential appropriateness of an evolutionary approach not only to the emergence of man and human societies, but also to contemporary human psyche and societies. Yet, altruism as studied by biologists is not what vernacular language calls altruism: some very "selfish" person (in ordinary language) who doesn't want to be "burdened" with children would be considered biologically altruistic because of her not having offspring; in contrast, a mother who sacrifices her entire life to her children, even though a paragon of vernacular "altruism," would be typically selfish from a biological point of view, since she is so entirely devoted to entities that share 50 % of her genes. Therefore, regardless of the outcome of the debate about units of selection, any principles extended from evolutionary biology to psychology must be checked as to whether they use vernacular or evolutionary concepts, and whether there is a risk of confusion due to ambiguous terminology.

Targets and Limits of Selection, 2: Limits of Selectionist Explanation: Adaptationism

Darwin stated that the phylogenetic tree life (the first principle of Darwinism) was partly explained by natural selection (the second principle), but that there were other mechanisms at work: "I am convinced that natural selection has been the main but not exclusive means of modification" (1859, p. 6). In this section we will turn to the actual limits of selectionist explanation as understood today in explaining both the form of the phylogenetic tree and the particular features of organisms.

The question of the limits and conditions of selectionist explanation has been central to the controversy about *adaptationism*. In a very influential paper, Gould and Lewontin (1979) described and criticized a pervasive method in evolutionary biology which they called the "adaptationist program." In short, adaptationists are those who think that the majority of important features of the living realm can be explained by natural selection (Sober 1994).

There have been many attempts to clarify the stance of adaptationism (Godfrey-Smith 2001; Lewens 2009). Maynard-Smith (1984) and Dennett (1995) profess adaptationism with some reservations; Gould (1980) and Wake (1991) do not. (Orzack and Sober (2001) present illuminating essays on the testability and the meaning of the adaptationist program.) For Gould and Lewontin (1979), the adaptationist program consists in first disassembling an organism into discrete traits and then building a selective history that establishes how each trait emerged as an adaptation to solve a particular problem. The authors criticize this program, contending that we cannot disassemble an organism any way we want, and that explanations of traits as adaptations are often untestable. Too often, they say, biologists, be they ecologists, paleontologists, or ethologists, create "just-so stories," namely, stories that invent a plausible scenario for the resolution of a hypothesized environmental problem – the trouble being that there is no way to prove that such a problem existed in the first place.

Gould and Lewontin point out that there is always the possibility of constraints on natural selection which prevent an optimal trait from being realized, even though it is also always possible to design models that postulate supposed environmental demands in order to derive as optimum the trait as it actually exists. By "constraint," theorists like them may mean various things (Maynard-Smith et al. 1985), so some clarification is needed. Constraints can be physical, such as the constraint on genome size which entails, e.g., obstacles to rapid metabolism within the cells of salamanders (Wake 1991); or, more obviously, the constraint that an elephant cannot have thin feet. Alternatively, constraints can arise from structural genetic arrangements; for instance, two genes might be too close to each other to be separated by crossover during meiosis. Constraints can be phylogenetic, meaning that selection acts on entities that have been shaped by their history and have inherited features that are difficult to change; for example, selection did not adapt vertebrates to life out of water by creating a perfect respiratory device, but instead modified the pre-existing devices of fish. Phylogenetic constraints become apparent in the course of comparisons across several species or clades: for instance the fact that giraffes, like all other mammals – including mice – have seven neck vertebrae indicates that the number of vertebrae is constrained; if it weren't, we would expect the number of vertebrae to be a function of size, and therefore more adapted. Moreover, phenotypes must be subject to genetic constraints, since there are pleiotropies that entail that a trait will, in any case, be accompanied by another trait that has no adaptive relationship to it.

Not least, constraints can be developmental, in which case they concern the range of variation available to selection. The issue of natural selection (of a given trait) facing constraints of this type is tightly bound up with the other issue raised by Gould and Lewontin, namely the impossibility of deconstructing living beings into discrete traits. The set of developmental constraints provides conditions for a kind of form which in its essence is untouched by selection, though always slightly altered and reshaped by it. Gould and Lewontin, following the German morphologists, of the 19th century call this the *Bauplan*. In this perspective, an organism cannot be seen as a mere bundle of adaptations, and selective explanations of all its traits do not suffice for a complete understanding of it (a claim echoed by a recent call for a "return of the organism" in evolutionary biology; Bateson 2005; Huneman 2010).

However, the emphasis on constraints is best understood in reference to the recently articulated evolutionary theory of development (Raff 1996; Arthur 1997; Gilbert et al. 1996). Selection acts on variants, but not all variants are able to develop from a given gene pool. The evolutionary theory of development unveils constraints on the rise of those variants which selection is about to act upon. For example, Wake (1991, pp. 547–549) showed that in all species of plethodontidae, the feet have got four toes instead of the five exhibited by their common ancestor, from which they derived by miniaturization. This change occurred several times in unrelated lineages, as an alternative state of developmental mechanisms sharply distinguished from the initial five-toes producing state: adaptive processes selected for size, whereas the developmental constraints led to the switch from five to four toes, independent of the lineage. This example has nonetheless been challenged by Reeve and Sherman (1993) in a defense of the adaptationist program. According to them, an appeal to selection is plausible even in Wake's case, since it is possible that there is selection at an embryonic stage that eliminates variants having more than four toes. The example illustrates that claims about developmental constraints may not be so easy to defend in the face of highly elaborated concepts and models of natural selection.

Clarification of this debate has been provided by Amundson (1994), who argues that developmentalists and selectionists simply do not ask the same question. Selection is appealed to in order to explain *why such and such variants arose and spread* in the gene pool among a given set of variants. By contrast, developmentalists try to answer the question of the *nature of this set of variants*: why are there these variants and no other variants, and to what extent is the emergence of certain variants unlikely or impossible? This, in fact, is not exactly a constraint on selection, because selection is an *explanans* to a different *explanandum* than the one developmentalists are interested in.

This acceptance of pluralism within the various explanatory strategies in evolutionary biology is likely to eliminate the false problems created by the adaptationist debates and leaves philosophers and biologists with the task of formulating and evaluating what could count as an adaptationist research program. Following

Godfrey-Smith (2001) and Lewens (2009), it is useful to distinguish between two major types of adaptationism: the *empirical* approach, which makes assertions about the pattern of the phylogenetic tree and the actual mechanisms of evolution, and the *methodological* approach, which contends that biologists must start out assuming the presence of adaptations, even if they recognize later on that in fact the predefined adaptational optima have not been reached and that constraints did exist. Such methodological adaptationism is justified for the same reasons for which the "phenotypic gambit" (cf. section "Genes, Dynamics, Optimality, and Strategies" above) was justified.

However, notwithstanding conclusions about the comparative values of the many adaptationist programs and hypotheses, there is a larger fundamental issue looming in the background to this question: namely, the conditions under which we are likely to recognize the effects of selection and its role in relation to other causes of evolution.

Selection, Drift, and Phylogenetic Inertia

Any model of real phenomena has to state a "null hypothesis," namely, the description of a state in which there is nothing to explain, and relative to which the actual state will have to be explained. (A more precise specification of the notion of a null hypothesis is given in statistics, where it plays a crucial role in hypothesis testing.) Many radical changes in scientific thought over the course of history have consisted in new definitions of a null hypothesis relevant to the subject of inquiry. For instance, Galilean physics began by conceiving of uniform rectilinear motion (as opposed to rest) as the null hypothesis, recasting acceleration or trajectory changes as the proper *explanandum*; the newly defined null hypothesis became known as the "principle of inertia."

By analogy, then, phylogenetic inertia suggests itself as the null hypothesis in evolutionary theory. In any population, traits have to be explained if they are not obviously the result of descent, i.e., if they are not homologous to traits in the ancestor species. Of course, the classification of traits as either homologous or not depends on the set of species under consideration. Thus, a preliminary specification of the set of species to be compared in order to account for traits in a given species is an absolute condition for applying the PNS. If traits are wrongly deemed homologous, due to inadequate specification of the initial set of related species to which the *explanandum* species is to be compared, this immediately entails false results (Orzack and Sober 2001).

However, methodologically, for a set of species, the relationships of homology and homoplasy implied by the statement of a null hypothesis are epistemologically related to the more fundamental *principle of parsimony*. (See chapter "▶ Quantitative Approaches to Phylogenetics," Vol. 1.) It can easily be seen that the more we judge there to be homologies, the fewer evolutionary lineages we need to draw on: this is a kind of parsimony, so Hennig's auxiliary principle – "Always presume homology in the absence of contrary evidence" – can be called upon if one subscribes to epistemological parsimony. But the stronger, ontological claim of parsimony also supposes this way of defining the null hypothesis.

Phylogenetic inertia, however, is not incompatible with selection. We have to distinguish between the question of the origin of traits, on the one hand, and their maintenance, on the other. When traits exist by phylogenetic inheritance but decrease in fitness in the new environment and the new species, selection is likely to suppress them or render them vestigial. In the reptilian family, this was probably what occurred as snakes went from four legs to none. Since origin and maintenance are distinct issues, selection and inertia are not two competing hypotheses but can serve as distinct *explanantia* for distinct *explananda*, and sometimes as complementary explanatory resources.

Proper definition of the null hypothesis is a methodological challenge in population genetics as well: since the Hardy-Weinberg equilibrium defines a kind of rest state of the population against which the effects of selection and other forces are assessed, it could be seen as the null hypothesis. However, it would also make sense to place randomness at the center of the null hypothesis. In that case, the null hypothesis for population change would be stochastic fluctuations, namely "genetic drift," as a consequence of the finite size of populations (drift being stochastic sampling error due to size). By contrast, if the HW equilibrium were the null hypothesis, drift would be a "force" or a "factor" of evolution, along with selection or migration, as the founding fathers of the Modern Synthesis called them.

It seems that the rise of neutralist theory in molecular evolution is leading to a switch in null hypothesis from the HW-based "rest state" to the random drift state (Veuille 2000). Yet, in support of the former hypothesis, one could appeal to Wright's concept of "adaptive landscapes" (see Gilchrist and Kingsolver 2001). The fact is that in a typical gene pool some combinations are local optima, and if a genotype is on the slope of such a local optimum, selection will lead it toward the peak. But there may be a fitness valley that separates it from another, higher fitness peak, so that its fitness will have to decrease first in order for it to reach the slope of that higher fitness peak. Only random drift, provided that the population is small, can lead a genotype through states of decreased fitness, across the fitness valley, toward the beginning of another incline – at which point selection can take over and lead the genotype toward the peak. Then, through migration, the new genotype can spread. In this model, drift helps to increase fitness by moving genotypes to global fitness peaks. Thus, besides natural selection, drift presents the other process accounting for the evolution of species, modeled by the travel of genotypes across fitness valleys and peaks. Wright named this schema the "shifting balance theory"; empirical evidence for its generality is sometimes given but is not always persuasive (Coyne et al. 1997) More recently, Lynch (2007) has argued that drift was a crucial factor in shaping the architecture of the complex genome of metazoans. In short, Lynch's argument is that these organisms, being quite large, lived in small populations, so that drift actually was very intense in the evolution of genomic features – as his models tend to suggest.

Issues Related to Patterns

Patterns: General Metaphysical Issues

There are many epistemological and methodological aspects to the construction of cladograms, and then a phylogenetic tree, presented in other chapters. There are also many issues surrounding the relationship between classification and phylogeny, and the proper understanding of classification: should it be cladist, pheneticist, or something else? The very idea of a phylogenetic tree is now challenged by the overwhelming importance of lateral gene transfer, which prevents systematists from entering conventional branches into trees (since with lateral gene transfer, transmission becomes horizontal; Doolittle and Bapteste 2007). Given the pervasiveness of lateral transfer in prokaryotes, these – as well as the archaea – may not give rise to a tree at all but be better depicted as networks. Lateral transfer aside, the idea of a tree of life raises important metaphysical issues concerning its interpretation. There are general questions about what is represented by the tree – which remain even if tree is not the proper classificatory scheme – and, more precisely, about the meaning of the nodes in the tree.

It is agreed that the nodes of a phylogenetic tree are taxa; authors often think they are species. However, the very meaning of "species" is controversial. Biologists have used different concepts here. Mayr (1970) famously proposed a biological concept of species defined by interbreeding (and non-sterile offspring). However, this definition fails to account for many things, including all prokaryotes and asexual species (which constitute the bulk of all biomass, the majority of living individuals, etc.). Others have proposed ecological concepts, phylogenetic concepts, etc. The metaquestion at issue is whether we should strive for a unique concept of species, or whether we can accommodate some pluralism. A further metaquestion concerns the metaphysical status of species (independently of what is the right concept allowing us to answer the question "Are x and y of the same species?"). Is a species, as traditional logic would have it, a *class*? Or did Hull (1978) come closer to the mark when he famously claimed that a species should be seen as an *individual* instead, made up of all the organisms of this species – an individual that has an outline, is spatiotemporally situated, is somehow integrated even though spatially discontinuous (just as many other individuals, like the USA, consist of spatially disjoint parts). Hull's notion better fits the structure of evolutionary biology. But to the extent that, on this view, species would be treated as genuine individuals, whereas other taxa would remain abstract entities, this discussion pertains to general debates about nominalism vs. realism.

Whatever the metaphysical status of species, the interpretation of phylogenetic trees compels us to make sense of the represented relations between species, and between taxa in general. Given that the relations in a tree reconstructed by systematists are not exactly a genealogy of organisms (Lecointre 2014), what is their logical status? Is it the hierarchical inclusion of species in a clade – and if so, why should this relation involve any diachrony (since inclusion is atemporal)? These are debatable metaphysical issues connected to the proper understanding of classification; it is an open question whether such issues are independent from commitments about the true concept of species, and commitments about the processes of speciation.

Evolutionary Scales, Development, and the Modern Synthesis

All of the issues investigated in section "Evolutionary Biology: Philosophical Issues Concerning Processes" above concerned selectionist explanations in general, whether applied to phenotypic changes in a population over a relatively short time period or to what Mayr (1959a) called the "emergence of evolutionary novelties" (such as the transition from the protostomes to deuterostomes). However, there is a significant difference in scale between those two objects of investigation, which raises another question about the scope of the selectionist explanations under consideration up to now. After Goldschmidt (1940), paleontologists distinguished between micro- and macroevolution: the former includes evolutionary changes in the population of a species, whereas the latter concerns the transformation of species and clades across time (which includes emergence of evolutionary novelties). The criterion for distinction between these two types of phenomena is speciation, which stands at their boundary. Patterns of macroevolution have been very controversial, especially because the Modern Synthesis, after Darwin, claimed that evolution occurred through cumulative selection of small variations, hence is *gradual*. A major issue with patterns is the extent to which gradualism can be said to hold in phylogenies.

This issue is closely intertwined with the question whether microevolutionary processes suffice to account for the attested macroevolutionary patterns. This remains an open question. For instance, it is plausible that Wright's "shifting balance theory" (cf. section 2.4.4 above) accounts for a lot of speciation on small time scales, but that its validity on a wider scale cannot be taken for ganted. Simpson (1944) argued that, even if macroevolution shows very different rhythms in different lineages, it nevertheless arises from the same processes as microevolution. In keeping with this view, Mayr (1965) established that gradualism – meaning that no evolutionary change is due to a single big mutation – is compatible with evolutionary novelties, since any change in function (like the exaptation of insect wings) or intensification of function (as in the evolution of eyes in some lineages) can account for many structural novelties. Yet Simpson felt compelled to introduce the concept of "mega-evolution," i.e., the emergence of new lineages; mega-evolution cannot so easily be characterized as a mere result of microevolution. (See chapter "▶ Patterns of Diversification and Extinction," Vol. 1.)

Eldredge and Gould (1972) were the most convincing proponents of a distinction between macro- and microevolution, which they captured in their paleontological theory of *punctuated equilibria*. This theory is, first of all, a reading of the fossil record that claims that discontinuity – sudden change after a very long period without major transformation – is not a result of geological lacunae (as Darwin tried to establish in Chap. 9 of the *Origin*). Instead, a dual-staged process is proposed to account for the fossil record: for long periods the fine-tuning action of adaptive radiation diversifies the species within a phylum, which is a kind of stasis, and then a quick general transformation of the body plan gives rise to a new phylum. While the first process can be dealt with by selectionist explanations, such as the ones considered up to this point, explanation of the second process – rapid general transformation – at a minimum needs to invoke a change in the conditions under which natural selection can operate, if we assume that no other process is needed.

Even though the idea of discontinuous change had been theorized earlier already as one possible kind of mode of evolution, namely "cladogenesis" (Simpson 1994), punctuated equilibria constituted a deeply challenging theory. The reason was that the configurational differences reflecting continuous vs. discontinuous change in the form of phylogenetic trees cry out for a matching difference in the nature or the conditions of the respective processes. If we subscribe to the idea of *Baupläne* as an integrated set of constraints, as advanced by Gould and Lewontin (1978), then we might think that phases of stasis represent fine adaptive tuning of existing *Baupläne*, whereas quick transformations represent the appearance of new *Baupläne*. The question of the status of macroevolutionary novelties associated with punctuations therefore entails the question of the explanatory sufficiency of the selectionist explanation schemes put forward by the Modern Synthesis.

Nevertheless, the concept of a punctuated equilibrium rests on some orthodox considerations of selection: among the founders of the Synthesis, Mayr (1965) emphasized the stabilizing role of selection, which, in a particular environment, largely eliminates big mutations since they are probably deleterious – given the high degree of integration of most organisms – and likely to threaten functional integrity. Periods of stagnation are, therefore, to be expected. The crucial point is the logical relation between large-scale and small-scale evolution. Fathers of the Synthesis, like Fisher and Wright, focused on microevolution. Yet some assumptions defining microevolution become false when we jump to macroevolution: first, environments are no longer stable and can change quickly and intensively; and second, the order of magnitude of the available phenotypic variation is different, since a much larger range of variation will be available if the time scale is bigger.

This second parameter is connected to evolutionary theories of development, and the focus on heterochronies crucial to Gould's *Ontogeny and Phylogeny*. Even though challenging the ubiquity of the gradual pattern of evolution claimed by Darwin and the Modern Synthesis does not *ipso facto* require challenging the traditional set of explanatory processes, evo-devo theorists assert that changing or extending this set of processes – especially by assigning development a role in evolution – is the necessary next move after acknowledgment of discontinuous patterns of macroevolution. It is these theorists who are mounting the main challenge to Modern Synthesis (Müller and Pigliucci 2011). The question they pose is: what are the constraints on the range of variation, and what constraints are about to change? Developmental constraints are likely to account for the observed limits on available variation, as well as for the restriction of the selection process to fine adaptive tuning and, finally, the puzzling outcome of stagnation in the evolutionary tree. If we want to understand the transformation phase, we have to turn to the modification of available variation and then to a possible change in constraints. Thus, if a modification of developmental mechanisms occurs, then we could expect an enlargement of phenotypic variation, a new field of operation for selection, and new evolutionary possibilities. If we assume that the features yielding this enlargement are deeply entrenched, we can understand that in this case selection will act upon many connected traits, at many levels of the developmental process, so that the result is likely to be a radical change in the existing body plan. This was Gould's (1977) point, following DeBeer (1958) concerning heterochronies: a change in the timing of development, involving many subsequent and connected transformations in the life cycle, is more likely to transform the body plan of a species than is a change in an adult trait. The important discovery of the regulatory developmental homeobox *(Hox)* genes reported in Lewis (1978), which are homologous in arthropods and chordates, supports this thesis: a slight change in expression of such a developmental gene, the Antennapedia gene, can give rise to a leg instead of an antenna in *Drosophila*. Even though genes of this sort (another well-known one is Bithorax) had been known since about 1915, a major stage in the emergence of evo-devo was the molecular characterization of these developmental genes in the 1980s (see Gehring 1998). Sequencing revealed that homeobox genes are homologous across several phyla. Setting aside the complexity of the cascades of interactions associated with these genes, the general idea is that great transformations of a *Bauplan* may be triggered by only slight modifications of some types of genes or of their expression channels (Arthur 1997), because these genes affect development and life cycles at many levels.

This empirical observation has set the agenda for other kinds of evolutionary research, including not only the attempt to construct a taxonomy of different mechanisms able to affect development and thus yield evolutionary novelties, but also the attempt to causally account for them – an agenda which is a part of the evo-devo program. Yet, as emphasized by Newman and Müller (2003), evo-devo does not reduce to an account of the evolution of developmental genes. It also comprises other research programs, ones that insist on sources of variation that may not be wholly genetic. These sources can be located at the level of organisms, as is the case with phenotypic plasticity, which was emphasized by West-Eberhardt (2003), who sees the behavioral plasticity that fits genetically identical organisms to different environments as a leading force in evolutionary change. Alternatively, they can be sought at a basic physical or chemical level, as illustrated by Müller and Newman (2005), who examine the evolutionary role of intrauterine motion in the production of phenotypes and determination of fitness, or by Newman (2013), who investigates the role of a small set of molecules whose combinations constrain possible variation because they include chemical dispositions of these molecules.

These challenges to the Modern Synthesis may concern not only the usual *explanantia* – by assigning to development, via developmental constraints, a major causal role in evolution – but also the *explananda*. For one, many authors characterize the Modern Synthesis vis-a-vis alternative approaches as focus on form vs. focus on genes (Pigliucci 2007), or as focus on structure vs. focus on function, following a traditional divide within biology (Amundson 2005). Yet a closer look at the issue of scale (macro- vs. microevolution) brings to the fore another contrast regarding *explananda*. Some clades are seen to persist for longer evolutionary periods than others; it is as if they had better capacities for evolution. It is often said of such clades that they are highly *evolvable*; the question, then, is what features make them more evolvable than others. At this large evolutionary scale, the issue may no longer be the evolution of adaptations (as responses to one environment at a time), but rather the *evolution of evolvability* itself. Greater variability obviously provides more evolvability; but other features such as modularity (Wagner and Altenberg 1996; Winther 2001) also play a role.

Switching *explananda*, then, could shift interest toward other levels of selection besides genes and individuals – for example, clades and populations – since some population-level traits, such as sex or a high level of polymorphism, quite obviously make a population more evolvable (Williams 1992). Shifting the scale of inquiry in the evolutionary tree expands interest beyond epistemological and methodological issues proper to selection to new objects and concepts – such as evolvability. It also raises genuinely new questions, for instance about the evolutionary origins of those features of traits that make them easily evolvable: should we seek the source of greater evolvability in the physical properties of a gene's DNA string, or in their modularity (Wagner 1995; Sterelny 2004) or redundancy from an information-thoeretic viewpoint?

Time Scales: Metaphysical Issues

The specifics of macroevolutionary patterns raise crucial issues about evolutionary processes and the current assessment of Modern Synthesis, but they also bring up some very general metaphysical themes, such as contingency, complexity, and progress.

Contingency

In *Wonderful Life*, Gould (1989) proposed profound implications for our view of life on earth from the recent findings of the Burgess Shale, analyzed in particular by Withington and Conway Morris. Gould's view was that many phyla appeared in the Cambrian, of which only few survived; thereafter, very few new body plans and phyla were really "invented" through evolution. But this creativity in evolutionary innovation is somewhat puzzling and raises a philosophical concern for the new *explananda* described above. Invoking the famous thought-experiment of the "tape of life" re-play, Gould suggested that the history of life contained an overwhelming number of contingent events, such as the mass extinction that killed more than half of the Burgess phyla (plausibly due to the impact of an asteroid, according to the Alvarez hypothesis).

The punctuated equilibria claim was only a weak challenge to an overall view of selectionism, since it can be reinterpreted as simply suggesting the need to define two regimens of selection – where the second one would include the aforementioned concepts and concerns stemming from developmental theory. By contrast, a view that gives a central role to contingency presents a strong challenge, since selection, and the adaptive capacities of individuals and species, cannot prepare them to withstand mass extinctions caused by excessively strong and rapid changes of environment – too rapid to qualify as what we call "selection pressures." Hence, individuals and species that survived the Cambrian mass extinction did not owe their survival to their higher fitness; the explanatory and predictive power of natural selection is very limited at this level of the history of life. The large, shrimplike *Anomalocaris*, for instance, seemed quite well fitted to its marine environment and was undoubtedly a strong predator – surely no less well adapted than the wormlike *Pikaia*, which seems to belong to the chordate phylum; nevertheless, *Anomalocaris* disappeared. Thus, major events are contingent with regard to the parameters ordinarily involved in natural selection.

However, confirmation of this "contingency thesis" rest on a lot of empirical elements that are not yet available. In particular, the exact interpretation of the Burgess fauna is still debated. Conway-Morris (1998) himself revised his original judgment and proposed that many Burgess phyla are in fact ancestors of already-known lineages. However, as Gould pointed out in his reply (Gould and Conway-Morris 1999), the point is not whether or not there are other mechanisms besides natural selection – a conundrum that we are currently unable to solve – but whether there were many more new phyla in the Cambrian, a great majority of which effectively disappeared. The contingency thesis relies on an affirmative answer to this question, which it should be possible to confirm by paleontological and morphological means. So, notwithstanding the strong challenge to selectionism, in Gould's view the important consequences for the interpretation of the history of life rely on empirical investigations. But the question is likely to be begged by methodological considerations involving *disparity*. If diversity refers to the variety of species, disparity refers to the heterogeneity of the body plans. Gould contends that whereas diversity may have increased in the Cambrian, disparity decreased. But even if we knew what the Cambrian phyla were, this would not entail the ability to measure disparity (Sterelny 2000). Most cladists assume that we can trace the genealogy of phyla but not evaluate the distance or difference between two phyla, because the criteria are always instrumental. In this view, Gould's thesis cannot be tested. The basic question, beyond the measurement of disparity, is the counting of body plans, and hence the definition of body plans. In the absence of any consensus about that issue, the contingency thesis, whether or not it is empirically adequate, is not likely to be tested.

Against Gould, Dawkins (1976, 1982, and elsewhere) has argued time and again, along with Dennett (1995), that even though the history of life is not repeatable exactly, in any "re-play" we would witness an evolution roughly similar to ours: an evolution of more and more complex entities displaying adaptations such as light detectors, motion detectors, energy-storage devices, manipulative strategies, etc. The idea is that even though the details of evolution are contingent, natural selection tends to always find the same kinds of solutions to the problem of living with environmental constraints, accumulating resources, and reproducing. Even if in different situations selection may find very different devices to realize these solutions, the solutions themselves (e.g., tracking prey through sensitivity to light, developing flexible behavior to accommodate variable environments, entering into collectives through kin selection or group selection; see section "Targets and Limits of Selection, 1: Levels of Selection" above) are constant. Contingency may play a huge role when one looks at the details of actual evolution on Earth, but, at a coarse-grained scale, comparing it to other, would-be evolutions would reveal constant "attractors" that organic life always tends to find. Documented instances of adaptive convergences suggest that this is indeed plausible: eyes have been invented 22 times independently, multicellularity has several independent evolutionary origins (Grossberg and Strathmann 2007), etc. But the reasons for convergences may also lie in structural features rather than adaptations (Conway-Morris 2010).

This debate has not arrived at a conclusion yet. But philosophers should emphasize that contingency and necessity may not be incompatible here, since the two theses do not seem to consider evolution at the same level. For this same reason, it is difficult to see what would empirically support one claim against the other in a conclusive way.

Complexity

A second pattern-related issue consists in the claim that evolution represents progress towards complexity. At first glance it does indeed appear true that more recent species are more complex; humans certainly are more complex than stromatolites or amoebas. Darwin himself, though, resisted the idea that evolution is progress: because it is based on natural selection, which is opportunistic and always builds on what already exists, evolution cannot be seen as the fulfillment of a teleological plan that leads to the highest level of perfection. (But see Richards (1992b) about Darwin's latent interest in a progressive view of evolution.)

It may be hard from today's perspective to make sense of the idea that evolution is oriented towards the emergence of mind, as has been often thought in the past, for example by paleontologist Teilhard de Chardin (e.g., de Chardin 1955). Yet even without a view towards a lofty endpoint of this kind, one can still have the intuition that there is some increase in complexity during phylogeny. This intuition is tricky to pin down in the absence of a clear concept of complexity and an operational metric for measuring it. Actually, many definitions of complexity exist, but it is hard to single out the one that would best suit evolution (see Adami (2002) on the variety of concepts of complexity and the lack of agreement). Dan McShea (2005) made some progress on this issue, by assuming a very simple notion of complexity as a measure of the number of distinct cell types, in an organism thereby linking complexity to diversity. Although this forces him to abandon the intuitive association of complexity and functionality – diversity is a purely structural concept – it allows McShea to show, first, that the phylogenetic record does indeed contain some patterns of increase in complexity, and second, that these patterns may occur without being caused by selection; they are simply due to the occurrence of variation (the concept of a "passive trend"). Brandon and McShea (2011) expand the idea into the concept of a "zero force law" in evolution, which states that even without external forces like selection working on it, complexity will tend to increase. When selection does come in, it will limit the observed complexity (and diversity). Whatever the ultimate fate of these proposals may be, they show that on the elusive issues of complexity, progress, etc., which philosophers have debated for centuries, one could in fact come to operational and testable claims in the context of evolutionary theory. This nicely brings us to our last section, about the ways philosophy itself may be affected by evolutionary theory.

An Evolutionary Framework for Philosophical Issues?

A philosophical focus on evolutionary theory cannot ignore the huge consequences that Darwinism had for traditional philosophical discourse, ranging from theological and moral matters to psychology. Conscious of the potentially huge philosophical implications of evolutionary theory's new insights into the descent of man, Darwin famously wrote in a 1838 notebook that "he who understands baboon would do more towards metaphysics than Locke."

Since these implications are as broad in scope as philosophy itself, instead of giving a complete but highly condensed survey this last section will highlight two or three general perspectives on both the fruitfulness and the difficulties associated with the use of evolutionary arguments in philosophical debates on human nature. Evolutionary theory now pervades the entirety of theoretical discourse on mankind: from philosophy of mind and language, to moral and social philosophy (Rosenberg 2003), to epistemology. Two general motivations can be distinguished: on the one hand, the promise of applying the power of selectionist schemes to problems outside biology (see Heams et al. (2014), part III); and on the other, the hope of integrating traditional problems of meaning and culture into an overarching evolutionary framework, which would permit philosophers to freshly approach questions about the origins of certain things (of ethics, of language, etc.) – questions that had been avoided because of the previously assumed non-testability of any hypotheses. This latter project defines a promising path toward naturalization, that is, towards a philosophical program whose goal it is to understand, by way of the natural sciences, objects that are supposedly unique to humanity: intentionality, cognition, ethics, etc.

Biological functions are intrinsically teleological and normative: traits are supposed to fulfill their function and are seen as abnormal when they do not; their reason for existence itself lies in their doing what they do (Millikan 1984). This normativity has often been understood through natural selection: a trait having function Y exists because it has been selected for, and it has been selected for due to its performing Y. Similarly, intentionality – namely, the property that mental states (beliefs, desires, etc.) are "about" something else – has been framed in this way, as having a function of covarying with some states of affairs (Millikan 1984; Dennett 1995; Longy 2014). Even truth itself, as a normative property (in the sense that to be true is a norm for uttering statements), can be understood from an evolutionary perspective: natural selection favors representations and beliefs that fit reality.

Ethical claims as well have been explained in evolutionary terms, by drawing consequences from the fact that altruistic trends may have been favored in humans – something that is even more powerful if the good of the group, having become internalized by individual agents, turns into a selfish motive for further actions

(Richards 1988; Clavien 2014). These and other consequences for intentionality, epistemology, and ethics will not be developed further here (but see chapter "▶ Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology," Vol. 3).

Selectionist Models of Culture and Science

As we have seen, there exists a general formula of selection that does not specify the replicators and interactors. Thus, provided that some cultural or moral entities are heritable, a selectionist scheme could render their initial creation, rise, and fall intelligible. Culture and science (as well as epistemology) are the most important *explananda* for those theories. It was noticed long ago that one human characteristic is culture. Recent research has highlighted forms of culture in many other vertebrate species (Danchin et al. 2011); the definition of "culture" ranges from mere social learning to symbolism, and the extent of the pervasiveness of culture across clades depends upon whether it is narrowly or widely defined. In any case, culture displays another kind of inheritance besides genetic inheritance: individuals learn and transmit what they have learnt, which appears somehow replicated. So, given that the transmitted items are likely to be slightly modified each time they are reproduced, a selectionist evolutionary account of culture might be feasible (Lewens 2008). (See chapter "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," Vol. 3.) However, an evolutionary account in this realm faces at least two big problems: the first one is the relationship between genetic and cultural inheritance. An entity may have great "cultural" reproductive success even though its bearer leaves no offspring. In that respect there is no necessary genetic basis for cultural traits; but if a cultural trait enhances the biological fitness of its bearer – as in the case of medical devices that cure illnesses – then this enhances the cultural trait's own reproductive success. The other problem is the definition of "success" in this context, given that cultural transmission is not only vertical as in biological heredity, but also horizontal (i.e., directed toward non-offspring); the horizontal dimension is at least as important as the vertical one for the spreading of a trait. Boyd and Richerson (1985) formulated a powerful set of models for cultural evolution. Although they did not make general assumptions concerning the genetic bases of cultural traits, it is clear that cultural evolution, with its vertical and horizontal dimensions of transmission, entails rather complicated relationships with genetic evolution.

Technology is an aspect of culture particularly amenable to an evolutionary approach, because the process of adaptation bears many parallels with technical evolution (Basalla 1988). In considering the rise of a certain technology (for example, photographic cameras), it is even possible to draw an evolutionary tree similar to a branch of the phylogenetic tree, with extinctions, radiations, privileged lines of evolution, and so forth. The growing field of evolutionary archaeology has undertaken such endeavor, showing that prehistoric tools can be arranged in a cladist taxonomy (O'Brien and Lyman 2002). Where technical evolution is concerned, variation is provided by changing fabrication technologies, and selection occurs since the more robust or efficient objects or processes are more likely to be copied. An evolutionary history of recent technology would resemble work in evolutionary economics, a program that applies selectionist schemes to firms and their management and technical "routines" (Nelson and Winter 1982).

Science is a specific area of culture subject to a specific constraint, namely, its aim to accurately represent the world in some way. The foundationalist program for philosophy of science, with its quest for a priori rules and guaranteed truths, declined in the 1960s, following extensive critiques. Philosophers after Quine turned to forms of so-called *naturalized epistemology*, i.e., an epistemology situated at the same empirical level as the sciences, which did away with the need for epistemically relevant norms to be knowable a priori. Evolutionary models of science, insofar as they use selection – in a sense which does not imply a trend among the selected entities toward any particular endpoint – do not presuppose any shared rationality or shared ideals among scientists, nor any special competence to recognize what is true. It is a fact that no definitive formulation of the goal of science – say, "objective truth" and the criteria to recognize it – has ever been reached; thus, we cannot presuppose that all participants in the endeavor of scientific inquiry are oriented toward the same goal. A selectionist process enables the rise of those theories with the tightest match to the real world, whenever theories bear any consequences in practical life; those consequences will be the effects upon which selection acts (Ruse 1986). At the price of giving up the idea that science aims at eternal and ideal truth (Giere 2001), evolutionary epistemology with a strong selectionist commitment, as originally formulated by Campbell and variously advocated by Giere (1990) and Hull (1988), gives a clear picture of the "process of science" that reconciles the lack of an empirically attested "aim" with the cumulative improvement of the fit between theories, data, and applications.

However, the nature of evolutionary units in this process is a confused issue: do these correspond to units of scientific content (suitably defined) and scientists, respectively? The clearest account of science as an evolutionary process is that laid out by Hull (1988). A key challenge lies in the need to prove that where theories are concerned, truth confers a kind of reproductive advantage, which is not obvious if the entities at issue are human beings. Giere's verdict (1990) is that, for the time being, evolutionary epistemology has a similar status as Darwinism did before its synthesis with genetics: it lacks an account of the mechanisms providing heredity and variation across individuals. However, such an account might be now provided by the cognitive sciences.

Like a selectionist theory of culture that is neutral regarding the biological foundations of cultural traits, evolutionary epistemology is not directly committed to any psychological theory about the *acquisition of knowledge*. There are some evolutionary theories using selectionist models that address this point, but these represent "evolutionary epistemology" in another sense: an "evolutionary epistemology of mechanisms" (EEM), distinguished by Bradie (1984) from the "evolutionary epistemology of theories" (EET) of science as a process. The two could be complementary (as in Campbell's Selection Theory of 1990), but they have no logical connection. In general, EEM can nevertheless be understood at an ontogenetic level or at a phylogenetic level. Since the EEM research program relies on an evolutionary representation of mind within nature, in order to figure out the philosophical issues at stake, the next subsection turns to the the strategy of building a continuous evolutionary framework for solving questions concerning the nature of man (see chapter "▶ Defining the Genus *Homo*," Vol. 3).

Evolutionary Psychology

Ever since Darwin's studies on the expression of emotions in humans and animals, evolution has been a resource for theories of mind and brain (Richards 1987). Evolutionary psychology appeared in the 1980s, replacing sociobiology, whose project consisted in applying to human behavior insights from the ecology of social behavior (kin selection etc.). Evolutionary psychology's explanatory strategy is to identify the adaptive value of features of *cognition* (e.g., Barkow et al. 1992). Since Tooby and Cosmides' formulation (e.g., in Tooby and Cosmides 1992), the guiding premise for this program has been, in brief: the human mind is made up of separate cognitive modules that quite unconsciously effectuate successful determinate algorithms that have been constituted through natural selection as adaptations during one of the longest periods of hominization, namely the Pleistocene. One famous example is the hypothesized "cheater-detection" module, whose supposed function it is to discover free-riders in situations of reciprocal altruism – situations that would have been frequent in the Pleistocene environment, and which have been analyzed in evolutionary game theory. Mating behavior and sexual dimorphism (e.g., Buss 1995; Symons 1979) are important subjects of this research program, which has also provided a robust explanation of some social cognition modules (Tooby and Cosmides 1992), such as our computationally amazing capacity to recognize faces, and our ability to represent what others think (called "Theory of Mind" (Chisholm 2003); see chapter "▶ Theory of Mind: A Primatological Perspective," Vol. 2). In linguistics new theories of the origin of language become available when one investigates the adaptive significance of communicating through systems of signs (Pinker and Bloom 1992; Desalles 2014; see chapter "▶ The Evolution of Speech and Language," Vol. 1).

One major assumption of evolutionary psychology is that the mind is at least in significant part composed of "domain-specific" algorithms – as opposed to the pervasive cognitivist hypothesis that the mind is run by generalist algorithms that apply across many domains, in the style of General Problem Solvers. This thesis fits in nicely with the evolutionary framework, because if cognitive competences are being modeled as answers to particular environmental problems, they are necessarily domain specific. Thus, evolutionary theory allows scientists to account for flaws or irrationalities of the mind described in the 1980s by the work of the economists Tversky and Kahneman (see Kahneman (2011) for review) as a lack of adaptation of our cognitive abilities to contemporary needs (since they were initially adapted to a very different environment). Similarly, evolutionary psychology offers a straightforward account for our highly developed ability to execute tasks generally unnoticed by traditional cognitivist psychology (e.g., face recognition). Not least, the claims of evolutionary psychology imply that cultural traits and institutions must be understood from a prior knowledge of psychological cognitive abilities (Tooby and Cosmides 1989a, b).

Evolutionary psychology faces several difficulties: the lack of information concerning the original Pleistocene environment (which leads to the rise of just-so stories), and, more generally, the pervasive invocation of adaptationism and the controversies about the extent of genuine modularity (Buller 2005). Above all, the entire program is in need of clarification of what is to be counted as a *trait*, since this decision affects all subsequent empirical investigations. Suppose that we are investigating the evolutionary significance of aggressive behavior: is aggressive behavior itself the underlying trait? Or is it one observed form of a general disposition that can manifest itself either aggressively or non-aggressively, depending on environmental factors? Or, could the observed behavior arise from a combination of various traits, such as envy, jealousy, territorial ambition, etc.? (Sterelny 2000). Unless this conceptual problem is directly addressed, the agenda of evolutionary psychology is likely to give rise to divergent, incompatible results with no principled way to compare their relative validity.

Conclusions

However interpreted, evolutionary theory is beset with theoretical problems concerning its major concepts (selection, fitness, adaptation). Those problems, while never dissociated from empirical biological issues, are at the same time philosophical, since they involve conceptual matters that imply epistemological and metaphysical choices. Although the problems of evolutionary theory cannot be solved independently of biological results, and above all could not have been formulated without reference to known facts of evolutionary biology, they are not likely to be solved purely within biological science itself. Reciprocally, their insightful articulation and attempts at solutions are of vital interest to the field of philosophy of science in general, as well as to metaphysics.

Surely the most tangible effect of evolutionary theory on philosophy is the opportunity it provides for elaboration of a new framework of inquiry about many philosophical topics – first of all, about the nature of man. This chapter intended to survey the objectives of current research programs in this realm, their variedness, and the difficulties they are facing. No integrative, synthetic knowledge of man, and no methodological framework for philosophical problems, has yet been established within the evolutionary perspective that parallels and is compatible with (and could ultimately be integrated into) the Modern Synthesis. For the moment, we have local results, new challenges, and insightful ways of approaching long-standing puzzles. But in the end, the broad rise of the evolutionary perspective will have profound consequences for the way we conceive of philosophical problems generally and, most of all, for our image of man – who is uniquely able to concern himself with those problems.

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Cooperation, Coalition, Alliances
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ Defining the Genus *Homo*
- ▶ Great Ape Social Systems
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Patterns of Diversification and Extinction
- ▶ Primate Intelligence
- ▶ The Evolution of Speech and Language

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The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology

Peter R. Menke

Contents

Abstract

This chapter aims to review the relevance of ontogenic data in an evolutionary perspective. Phylogenetic investigation through developmental information is one of the most promising avenues to the elucidation of our natural history. First, the problematic integration of biological subdisciplines into the evo-devo synthesis is considered: the homeobox as Pandora's box is discussed and the important role of a comparative morphology program is emphasized. Second, the study of development reveals essential aspects of primate supraordinal relationships and does not support an archontan reality. A special note defines the traditional superorder Archonta as (1) an artifact of the *Scala naturae* concept, since archontans were supreme public servants of the Greek ancient world. On the other hand, it is (2) a vehicle to explain the existence of flying mammals (Chiroptera) via a gliding intermediate stage (Dermoptera). Third, the

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P.R. Menke (✉)
Institut für Anthropologie (1050), Johannes Gutenberg-Universität Mainz, Mainz, Germany
e-mail: pmenke@gmx.de

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impact of neotenic ideas on paleoanthropology is retraced, and current contributions describing the evolution of the human cranial base and bipedalism are presented. Man's domination by neoteny seems to be a *burlesque*, accurately related as pithecocentrism.

> *Partout où quelque chose vit, il y a, ouvert quelque part, un registre où le temps s'inscrit.*
> *Henri Bergson*
>
> *Bestimmt sich nicht auch unsere Erwartung und unsere Bereitschaft, das Neue zu hören, notwendig von dem Alten her, das uns schon eingenommen hat?*
> *Hans-Georg Gadamer*

Introduction

The polymath Johann Wolfgang von Goethe was fascinated by the anatomical diversity of the animal kingdom and its variability of form. In 1817 (11 years before Karl Ernst von Baer published his embryological manifesto), he wrote:

> Man findet daher in dem Gange der Kunst, des Wissens und der Wissenschaft mehrere Versuche, eine Lehre zu gründen und auszubilden, welche wir die *Morphologie* nennen möchten [. . .] Er abstrahiert bei diesem Ausdruck von dem Beweglichen, er nimmt an, daß ein Zusammengehöriges festgestellt, abgeschlossen und in seinem Character fixiert sei. Betrachten wir aber alles Gestalten, besonders die organischen, so finden wir, daß nirgend ein Bestehendes, nirgend ein Ruhendes, ein Abgeschlossenes vorkommt, sondern daß alles vielmehr in einer steten Bewegung schwanke. . ..[1]

Life is obviously not a static arrangement but the particular result of a dynamic, ongoing process. This phenomenon is nowhere more relevant than for ontogenetic studies.

This review approaches some important aspects of ontogeny and phylogeny by presenting a selection of studies that exemplify this scientific field. Embryology, comparative anatomy, and especially molecular biology demonstrate an amazing unity among organisms, and sometimes, bizarre variations among them stem from a series of basic themes, some of which are common to all living beings (Nielsen 1995). I concentrate here on broader matters, such as (1) comparative embryology, especially with regard to K.E. von Baer and its modern derivative: evolutionary developmental biology. The ancient realm of morphology plays a major role in this context.

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[1] "It can be observed that in the course of art, knowledge, and science, several efforts are made to create and cultivate a doctrine that we may call *morphology*. . .One abstracts the reality of fluctuation by supposing that a belonging together and a fixation of its character can be fulfilled. Considering all shaping, especially in organic forms, we can state that there is no stability, no resting or completing-but rather a fluctuation of all phenomena" (pp 55, my translation and emphasis).

By the 1980s, molecular biology and paleoanthropology had developed their own concerns and controversies. Yet the significance of studies going beyond the analysis of adult phenotypes was already necessary and self-evident (Howell 2002).

Since hominin fossils, such as those from Dikika, Taung, Mojokerto, Nariokotome, Tešik-Taš, Kiik-Koba, or Le Moustier, represent infantile or juvenile stages, studying our phylogeny via ontogeny should be of particular importance, although, as Krovitz et al. (2003) pointed out, juvenile fossils are lacking for most species in the genus *Homo*. Here, therefore, studies are reviewed that are based on (2) embryological data sets. Generally, the methodological approaches taken to the analysis of the ontogeny of modern individuals and the fossil record differ strongly and accordingly have different meanings for the study of evolution (MacPhee 1981).

Focusing mainly on current primatological and paleoanthropological aspects, the far-reaching influence of (3) Bolk's fetalization hypothesis is retraced. Gould's (1977) interpretation is reconsidered (4), based not only on modern studies but also on traditional work that nowadays maintains only a shadowy existence, although its explanatory power is astonishing. As one may well imagine, any review of the ontogeny-phylogeny question must at present be incomplete. However, *gutta cavat lapidem, non vi sed saepe cadendo* (constant dripping wears away the stone).

Comparative Embryology and Evolutionary Developmental Biology

Karl Ernst von Baer and *Gallus domesticus*: The Beginnings of Comparative Embryology

Nineteenth-century comparative embryology lies at the origin of evolutionary developmental biology or, more briefly, *evo-devo*. Von Baer's and Haeckel's works are the most popular examples of that period, and these authors' "laws" describing the general development of organismic form are of great interest.

Karl Ernst von Baer, a pupil of Ignatius Döllinger, a professor at Würzburg, is known as the founder of embryology as a scientific endeavor. Although representatives of German transcendentalism had provided some insights into the field of embryology, it was only in 1828 that von Baer's *Über die Entwickelungsgeschichte der Thiere: Beobachtung und Reflexion* appeared in print and made even contemporaries recognize him as the founder of embryology. In the first volume of his masterpiece, von Baer concentrated on the development of the chicken (*Gallus domesticus*), but he also bore general laws of development in mind. He worked with dissecting needles and a simple microscope: the "Scholia" describe the deductions he made. The accuracy and minuteness of his fundamental observations is absolutely astonishing. Russell (1982, p. 114) was unable to hide his admiration: "His account of the development of the chicken is a model of what a scientific memoir ought to be...."

Von Baer's ideas incorporate the truly important distinction between the *type* (Wiesemüller et al. 2002) of organization (the structural plan) and the *grade* of differentiation (modifications of this plan). The aim of comparative anatomy to reveal group-specific *Baupläne* now had a prominent new tool by integrating embryological data.

As Charles Darwin was not a professional morphologist, it was others who introduced evolutionary thinking into the realm of comparative embryology. Ernst Haeckel's formulation of the biogenetic law (ontogeny as the short and rapid recapitulation of phylogeny) presents a radicalized phylogenetic approach. Recapitulatory ideas were not new since Müller (Russell 1982) had already supported a similar hypothesis in 1864. Yet Haeckel's verve and passion – very striking in a commemorative speech in 1909 (*Das Weltbild von Darwin und Lamarck*), on the occasion of the 100th birthday of Charles Darwin, favoring Goethe's monistic world view as being the *ultima ratio* – made it famous. The interpretations of *heterochrony* and its implication for paleoanthropology are discussed later on. However, how does today's evolutionary developmental biology reflect the ideas of von Baer and Haeckel?

The Newcomer: Evolutionary Developmental Biology

Von Baer and Haeckel: Outmoded?

The fancy term *evo-devo biology* represents an emerging field (Gould 2002; Carroll 2005) that has been specially featured in semipopular journals such as *PNAS* (2000) or *Nature* (2003). It refers to the quest by evolutionary biologists to understand how organisms change shape and form. Hall (2002, p. 8) explained that "... evolutionary developmental biology is more than a name for an emerging subfield of biology. It is a reflection of a level of analysis, synthesis, and understanding not possible through the study of evolution or development alone."

So how are the laws of von Baer and Haeckel interpreted nowadays? Gould (1977) supported von Baer's explanation and regarded it as being essentially correct while Haeckel's law is incorrect. Arthur (2002, p. 757) disagreed and argued that when comparisons are made between different levels of complexity, a pattern emerges that is broadly (although only in a very imprecise way) recapitulatory. The *déjà vu* occurs by recapitulating levels of complexity rather than precise morphological details. Haeckel and von Baer are both right in assuming that "evolution leads both to embryonic divergence and, in some lineages, to a lengthening of the ontogenetic trajectory leading to more complex adult phenotypes with greater numbers of cells, their embryos passing through simpler, quasi-ancestral forms."

Sander (1983) defined a "phylotypic" stage by describing a point of maximum similarity and a succeeding period of divergence. In this scheme, von Baer's principle of divergence only applies after this stage. Richardson et al. (1997) revealed a phylotypic period, rather than a stage, by screening more vertebrate species: this supports a broader comparative view. The hourglass model of development (Duboule 1994) might prima facie have reduced the explanatory power of von Baer. We should, however, be aware that this is a different kind of hourglass, the point of constriction being close to the beginning (Richardson 1999).

Homeobox: Pandora's Box for the Integration of Biological Subdisciplines?

Lewis (1978), Nüsslein-Volhard and Wieschaus (1980), and others (see also Lemons and McGinnis 2006) have revealed the meaning of *homeobox* genes and their importance for investigating the *Baupläne*. One application of this discovery which causes headaches for many scientists (Kuratani 2003) is the vertebrate cranium: is it a novelty that lies anterior to the head of a prevertebrate organism, or is it homologous to a special region of the amphioxus nerve cord? Holland et al. (1992) recognized a homology based on a comparison of expression patterns of *AmphiHox 3* (an amphioxus *Hox* gene) and *Hox-2.7* (the supposed mammalian homolog) and consequently denied the vertebrate brain as representing a novelty of the animal kingdom.

Hillis and Moritz (1990, p. 502) emphasized that the power and the rapid development of these techniques "has produced an euphoria in evolutionary biology, because so many new problems can be addressed, it is a commonly held misconception that all evolutionary problems are solvable with molecular data...." Nielsen (1995) worried that without morphological characters, the molecular data can produce only "naked" trees. Müller's (2005) review explained inter alia the importance of a comparative morphology program as a prerequisite for an evo-devo synthesis.

Furthermore, Conway Morris (2000, p. 4429) warned about "the risk of losing the overall evolutionary context. [...] Not only that, but there are intriguing mismatches between genomic architecture and bodyplan complexity." He pointed out that in all likelihood, a substantial proportion of the metazoan genome was available well before the Cambrian explosion and that a corresponding genetic architecture of genes and bodyplans is required, although he admits that we are still far from understanding either their interconnections or evolution. Arthur (2002) also met the challenge by demonstrating the change of tendency from general laws to specific pathways. He thus called attention to emerging concepts that integrate the overwhelmingly complex data.

As there is no one-to-one correspondence between genotype and phenotype, another important aspect of the problem lies in the interaction of genetic and nongenetic factors that act in different ways upon gene expression and create phenotypic diversity during development and evolution (Hall 1990, 1998b, 2002). Thus begins an appreciation of epigenetics. Goodwin et al. (1983), Raff (1996), and Hall (1998a, b, c) have called attention to the fact that change in development and evolution must be considered as an interaction of several "biological levels" so that consequently a hierarchical structural analysis is needed.

The timeless stimulus of Carl Gegenbaur – once called the most important morphologist in the world – and his legacy for the twenty-first-century evolutionary developmental biology lies in his methodological reflections about the relationship between embryology and comparative anatomy. Gegenbaur's emphasis of careful and detailed observation over tempting and far-reaching speculation should be the aurea mediocritas (the golden mean) in our fast-moving world. The modern scientific endeavor faces therefore similar challenges to those of the nineteenth-century evolutionary morphologists, "namely to distinguish between several possible phylogenetic scenarios" (Laubichler 2003, p. 29).

As to the formal integration of evo-devo with neo-Darwinian theory, not much progress has yet been made. The way toward a unified theory, however, seems to be open, and the stimulation of the biosciences through evo-devo biology is quite evident (von Dassow and Munro 1999; Müller 2005).

Primates and Supreme Public Servants of the Greek Ancient World

Primates and Their Supraordinal Relationships

Although primate origins and supraordinal relationships are discussed twice in Vol. 2 (chapters "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence" on morphological and "▶ Molecular Evidence on Primate Origins and Evolution" on molecular data), I would like to mention some studies that have used ontogenetic data in this context. According to Hofer, one of the ultimate goals of primatology (Spatz 1964) is the elucidation of the phylogenetic position of primates compared to other mammals. Gregory (1910) formulated the concept of the Archonta, which unites Chiroptera (bats), Dermoptera (colugos), Menotyphla (Macroscelidea, elephant shrews; Scandentia, tree shrews), and Primates into one single superorder. Later on, modified versions of this hypothesis excluded the Macroscelidea (Novacek and Wyss 1986), while Adkins and Honeycutt (1993) surprisingly favored a revival of this grouping based on molecular data (*COII* gene). Even after the Hennigian revolution (1950), many morphologists confirmed the traditional version of primate supraordinal relationships by defining synapomorphies (Hooker 2001). Noncladists, such as Szalay (Szalay and Drawhorn 1980; Szalay and Lucas 1993), supported the evolution and diversification of archontans in an arboreal milieu. The approach is based on the aim of "Darwinian evolutionary classification" to include both adaptive similarity and monophyly sensu Bock and von Wahlert (1965). Critical comments can be found in Grande and Rieppel (1994).

Murphy et al. (2001), however, proposed the new superorder "Euarchontoglires," based on nuclear and mitochondrial gene sequences of 42 placental specimens. This new grouping (Asher et al. 2005; Nishihara et al. 2006) consists of the Euarchonta (= Dermoptera + Primates +Scandentia) and the Glires (= Lagomorpha + Rodentia). Surprisingly, bats are excluded and do not seem to be closely related to primates. MacPhee (1993, p. 372) already noted (based on Adkins and Honeycutt 1993) that ". . . something is pulling the rodents toward the primates in this data set. . .."

These radical changes in primate supraordinal relationships consequently deny the Volitantia hypothesis (Illiger 1811), which favors a sister group relationship of bats and colugos (Leche 1886; Thewissen and Babcock 1991; but see Beard 1993).

Wible and Martin (1993) documented that the ontogeny of the tympanic floor and roof does not provide any characters distinguishing all extant archontans from other eutherians. Actually, Archonta (archontans were supreme public servants of the Greek ancient world) has *Scala naturae* written all over it and represents a vehicle to explain the existence of flying mammals (Chiroptera) via a gliding intermediate stage (Dermoptera) in the absence of appropriate fossils (see also Sears et al. 2006). It should be emphasized that the concept of *Scala naturae* was long developed *before* the theory of natural selection (Martin 1973). Darwin (1859) promoted the view that nature does not make leaps – natura non facit saltum – in order (1) to fill the gaps in the fossil record and (2) to strengthen his intellectual position (Schwartz 2000). Although Darwin's motives are plausible, accepting the Volitantia concept might be an immediate consequence of the emerging battle against supporters of divine creation. Rasmussen (2002, p. 7) specified in a more diplomatic manner: "However, it is fair to say that at this juncture we do really not know if primates are more closely related to Scandentia, Plesiadapiformes, Chiroptera or Dermoptera. These four orders are conveniently lumped together as 'archontan' in what may be a true clade but which for lack of unambiguous evidence is often used as an informal grouping." *Faute de mieux:* chimeric archontans? (see also Hardt et al. 2006; Menke and Henke 2008). In the context of primate evolution, some important examples of cranial and postcranial anatomy are presented here.

The Myth of Primate Entotympanics: Consulting Embryological Data and Its Phylogenetic Implications

It is now more than a century since embryological studies [the Reichert-Gaupp theory, refuted by Otto (1984)] demonstrated the homology of the mammalian malleus and incus with the articular and quadrate bones which formed the ancestral jaw joint of gnathostomes. This tremendous transition can be traced in fossils by comparing basal synapsids through therapsids to early mammals. A fetal mammal shows that the angular (tympanic), articular (malleus), and quadrate (incus) develop in the same positions they occupy in the cynodont skull (Allin 1975; Maier 1987). The importance of new fossils (Rich et al. 2005), however, is demonstrated by Martin and Luo (2005): the separation of the middle ear bones must have evolved independently among the therians and the monotreme mammals. The middle ear and surrounding basicranium have played a decisive part in mammalian systematics over the past years (e.g., Sánchez-Villagra et al. 2002).

In 1979 – 2 years before the *Auditory Regions of Primates and Eutherian Insectivores* was published – R.D.E. MacPhee presented a new interpretation of the disputable issue of "primate entotympanics." Not all mammals show these mysterious skeletal elements. As otic characters are essential for primate taxonomy, this was a potential criterion for distinguishing primates from their relatives [e.g., colugos (Fig. 1) and tree shrews]. Mivart (1881) defined this specific element as "entotympanic," while Wincza (1896) introduced the term "metatympanic" (van Kampen 1905). A few influential morphologists (van Kampen 1905; van der Klaauw 1931) already championed the existence of primate entotympanics.

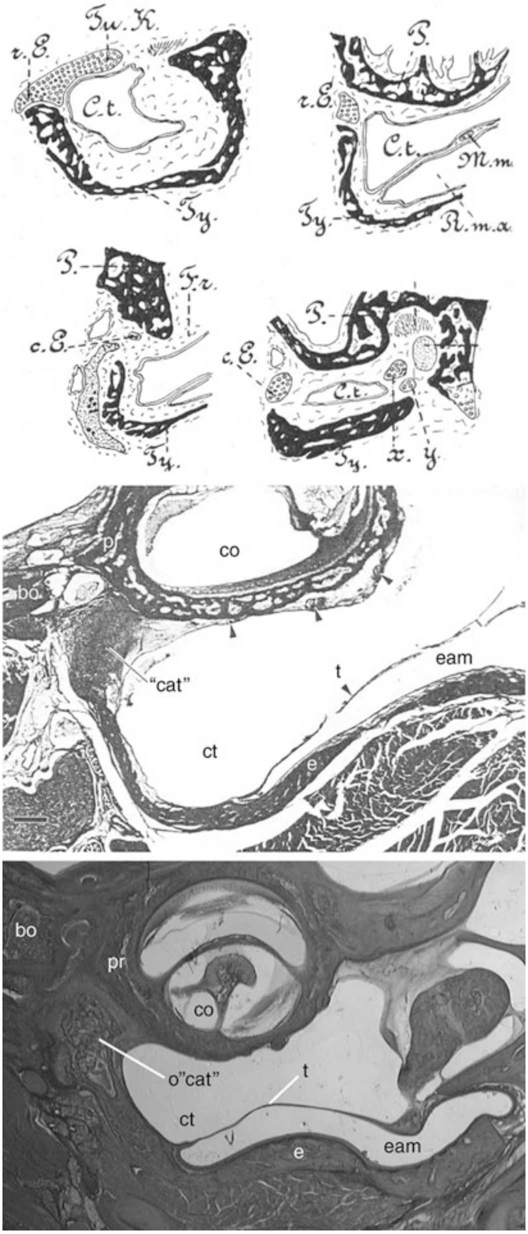

Fig. 1 *Top*: fetal *Cynocephalus volans* (Dermoptera). Cranial length 41 mm, frontal section. Note the entotympanics. *c.E* caudal entotympanic, *C.t.* cavum tympani, *F.r.* fenestra rotunda, *M.m.* manubrium mallei, *P*Petrosal, *R.m.a.* recessus meatus acustici externi, *Tu.K.* tuba auditiva cartilage, *Ty* tympanic, *x,y* cartilage. Sections have a thickness of 25 μm. Not to scale. (Modified from van der Klaauw 1922). *Center*: late-fetal *Cynocephalus variegatus* (DUCEC 806). Crown-rump length 136 mm. It shows a frontal section through the promontorium in front of the tegmen

Van der Klaauw (1922) published an ingenious work (*Über die Entwicklung des Entotympanicums*) in which he made a strong case for two different types of entotympanic, rostral and caudal. Developing in the anteromedial corner of the membranous tympanic floor, the rostral entotympanic grows posteriorly. Unlike the tympanic processes, entotympanics grow and develop within the fibrous membrane of the tympanic cavity (MacPhee 1979).

Starck (1975, p. 143) reported for *Tarsius* that the existence of an entotympanic is not yet proven. In the younger stage, the tympanic region does not show any peculiarities and an entotympanic cannot be detected. However, an older specimen showed a floor of the middle ear cavity that is formed by endochondral bone. It was closely connected with the otic capsule, but it showed a rostral extension near the auditory tube: "The ossified bone still contains some cartilaginous tissue, and this *would indicate the presence of a true entotympanic*, since the petrosal components of the floor are usually formed by periosteal bone. These results are in accordance with the findings of van Kampen (1905)" (my emphasis). According to MacPhee (1979), primate tympanic floor elements do not develop like any known entotympanic but, rather, like other tympanic processes. Prenatal *Microcebus* demonstrates secondary cartilage in the rostral tympanic process of the petrosal, which is interpreted as an embryonic adaptation – the explanation of the primordial fusion of once separate entities is no longer required. The hypothesis of a suppressed entotympanic is made more unlikely by the endochondral development of the caudal tympanic process of the petrosal (contra Starck 1975). To quote MacPhee (1979, p. 43): "Therefore, with regard to the constitution of the primate ventral wall, and with some necessary violence to Newton's quip, *non fingo ossa* – I posit no bones." *Eureka*, a new primate characteristic was identified via the careful interpretation of ontogenetic data.

Postcranial Ontogenetic Data and the Origin of Primates

Stafford and Thorington (1998) and Hamrick (2001) presented important data on the hand proportions in developing and adult mammals. Using a ternary plot (Hamrick 2001), relative metacarpal, proximal, and intermediate phalanx lengths among fossil and extant taxa deliver an elegant possibility of distinguishing primates from other "archontan" mammals. Primates differ from flying and gliding

Fig. 1 (continued) tympani. *Arrowheads point* to branches of the internal carotid nerve running in a transpromontorial position. Scale bar = 0.33 mm. *"Cat"* fused cartilage of the auditory tube and rostral and caudal entotympanics, *bo* basioccipital, *co* cochlea, *ct* cavum tympani, *e* ectotympanic, *eam* external acoustic meatus, *pe*Petrosal, *pr*Promontorium of petrosal, *t* tympanic membrane. (Modified from Wible and Martin 1993, © Plenum Press.) *Bottom*: the next step. Frontal section of a juvenile *Cynocephalus volans* specimen, of 145 mm crown-rump length, from the collection of the Institute of Systematic Zoology in Tübingen. It illustrates the ossification of the fused cartilage of the auditory tube and the rostral and caudal entotympanic (*o"cat"*). Hunt and Korth (1980) reported but they did not illustrate the fate of this important anatomical detail. Sections have a thickness of 40 μm. Not to scale mammals in having much longer proximal phalanges relative to their metacarpals and are unique among the sampled mammals in having elongated proximal phalanges relative to their metacarpals. A comparative analysis of hand development in the mouse lemur *Microcebus murinus* and other meta- and eutherian mammals reveals that "interspecific variation in relative digit and metapodial proportions has high-developmental penetrance; that is, adult differences are observed at early ontogenetic stages" (Richardson 1999, p. 348). Hamrick's (2001) results suggest an evolutionary scenario that describes an "invasion" of the fine branch niche based on a hand with a short palm and long fingers yielded by a change in digital ray patterning and segmentation.

Recent advances in developmental genetics elucidate patterns of postcranial growth in primates. Another study is based on a comparison of developmental data of CD1 mice fetuses and Rhesus macaques: Hallgrímsson et al. (2002) demonstrated the evidence for morphological integration of the limbs as serially homologous structures by reporting the covariation structure of forelimb and hindlimb skeletal elements. This proves that link structures between the limbs are caused by developmental modules, producing the covariation that would be needed to be overcome by selection for divergence in fore- and hindlimb morphology.

Since primates have more distally concentrated limb mass than most other mammals, Raichlen (2005) studied the unique kinematics of primates by testing a longitudinal ontogenetic sample of baboons (*Papio cynocephalus*). He concluded that the evolution of primate quadrupedal kinematics was tied to the evolution of grasping hands and feet.

The Impact on Paleoanthropology

Bolk's Fetalization Hypothesis: Its Successors and Critics

Forever Young?

Many contributions have emphasized the relevance of phylogenetic conclusions from ontogenetic information (Minugh-Purvis and McNamara 2002). One of the most influential books on developmental change and (human) evolution is Stephen Jay Gould's *Ontogeny and Phylogeny* (1977). Tuttle's (1978, p. 287) review of this book was not rhapsodic: "Perhaps the author attempted too much in this chubby volume [. . .] Time will tell whether it is in fact a hemicentennial classic as implied on the dust jacket." Well, in the meantime it has become probably one of the most frequently cited compendiums. Howell (2002, p. xi) commented that "its effect was immediate, substantive and far-reaching." Looking briefly at the bibliographies of modern studies often gives the impression that the consideration of developmental change in human evolution began in 1977 (Coqueuniot et al. 2004). Here, I focus partly on some of the "ancient" morphological studies that negate "essentially neotenous" ideas, to show how profound their explanatory power really is.

Why assume an *impact* on paleoanthropology? The ideas of Louis Bolk, a Dutch anatomist, have in fact had an enormous influence on scientists working in many different fields. The paleontologists Beurlen and Schindewolf (1936, 1950) supported a phenomenon called "proterogenesis" by pointing out that some evolutionary lineages that are present in successive strata may be interpreted as a process of maturing of former embryonic or postembryonic form levels. I mention these thoughts – although they do not deal with anthropological questions – because they show that Bolk's thoughts are part of a greater, speculative construct of evolutionary ideas. Portmann (1960) already assessed the situation by claiming that criticism of Bolk's considerations has to be criticism of the entire construct and argued that it is still in progress and may not be considered completed.

As Starck (1962) argued, Hilzheimer (1926, 1927) and others have pointed to morphological and physiological data to explain the principle of fetalization. Starck (1962) traced the hypothesis of neoteny back to Strickland and Melville (1848), but Bolk was the one who applied it to human evolution. A sequence of papers (the version of 1926 being the most frequently cited) takes us away to a non-Darwinian construct. So which are the essential elements?

Bolk (1926, p. 5) split human characters into (1) primary and (2) consecutive features. Primary characters are those products of developmental factors that caused the origin of human morphology. Consecutive characters, on the other hand, are phenomena of bipedal adaptation. Hence, the primum mobile of human evolution is not bipedalism, the "secondary" characters of which strictly follow functional aspects. Bolk (1926) considered the primary human characters to be the (1) reduction of body hair, (2) form of the external ear, (3) epicanthic eye fold (Mongolian eye fold), (4) loss of pigmentation in skin, (5) orthognathy, (6) foramen magnum in a central position, (7) a long persistence of cranial sutures, (8) subcerebral position of orbits, (9) high relative brain weight, (10) position of the spinal column relative to the cranial cavity, (11) women's labia majora, (12) structure of hand and foot, (13) form of the pelvis, (14) women's sexual canal in a ventral position, (15) multipapillary kidneys, and (16) the branching pattern of the arch of the aorta [the last two characters are not mentioned by Gould (1977)]. What is the common denominator of these characters?

The characters listed by Bolk are phenomena which temporarily appear during primate ontogeny. Although Bolk (1926, p. 44) differentiated the problem by separating (1) the relatives of *Homo sapiens* and (2) the development of human shape, as Slijper (1936, p. 504) explained, he advocated the idea that our ancestor must have been an *extant*Primate species. Characters of human fetalization consequently represent persisting ontogenetic primate characters. Human ontogeny therefore demonstrates conservative traits, while humans' primate ancestors showed "propulsive" (advanced) characters. Bolk's (1926, p. 26) bottom line is *H. sapiens* represents a sexually mature primate fetus. However, how did he explain the inhibitive force that fixes man's physical appearance at a certain point in time?

"The obvious answer is: The slow progress of his life's course" (Bolk 1926, p. 470) and the fact that "human life progresses like a retarded film" (Gould 1977, p. 360). Bolk (1926, p. 38) asserted that the development of dentition, consciousness, and the late closure of cranial sutures act as indicators of a dominant retardation phenomenon. The chain of causes starts with the modification of the endocrine gland function (for a modern hypothesis, see Crockford 2002) by *internal* alteration, not by external factors of the environment (Bolk 1926, p. 22).

Slijper (1936), another Dutch scientist, published an outstanding analysis that considered cetacean relationships, the fetalization hypothesis, and the clarification of fundamental terms. Ironically, Gould (1977, p. 365) called Slijper's criticism "famous," which is quite euphemistic since even the German-speaking Starck (1962) complained about it as not being easy accessible and often ignored. One major problem of Bolk's idea is the *subjective* splitting of primary and consecutive features. Slijper (1936, p. 509) recapitulated Bolk's scientific career and stated: "... we get the impression that Bolk did not present primary characters (mostly human) at first and discovered their fetal character afterwards, but rather observed a contrarian procedure: he discovered fetal characters and defined them subsequently as primary. This explains the remarkable correlation of primary features with fetal phenomena and diminishes its objective value" (my translation). Slijper also denied any general neotenous influence on human ontogeny.

Two prominent morphologists concerned with primordial cranial studies were Benno Kummer and Dietrich Starck. In 1962, they published the first modern study on fetal *Pan troglodytes* (Fig. 2). Starck and Kummer followed Hofer (1958, 1960) in distinguishing basal and prebasal kyphoses. Gould (1977, p. 378) excellently summarized their findings thus: (1) All fetal mammals have a prebasal kyphosis at the junction of the presphenoid and ethmoid bones (a bending with the concave side toward the body, as opposed to a lordosis). (2) This kyphosis decreases during ontogeny, the sphenoethmoidal angle opens out, and the face comes to lie in front of the cranium. (3) While the prebasal kyphosis develops within the basicranial axis during human ontogeny, a different kyphosis develops between the basisphenoid and presphenoid bones at the level of the dorsum sellae. This second kyphosis produces a secondary decrease in the sphenoethmoidal angle following the earlier increase conditioned by straightening of the prebasal kyphosis. (4) The "fetal" value of the sphenoethmoidal angle in human adults does not reflect the retention of a fetal condition but arises from development of the new, sellar kyphosis. It is a new feature – not a paedomorphic retention.

Amazingly, Gould (1977, p. 379) concluded: "These authors have used this single contention as the basis for a campaign against the hypothesis of fetalization..." A single contention? *A campaign*? To be blunt, Gould himself started a campaign. In relation to Bolk's explanation of skull development, Portmann (1960, p. 586) already commented that "... skull development is a complex issue which makes Bolk's solution suspicious" (my translation). Reflecting the development and evolution of the human chin, Vogel (1964) warned against too "localized" a view and called for the consideration of the complexity and interaction of *all* developing skull components. Schwartz and Tattersall (2000) revisited the presence of a chin in hominins and examined the importance of developmental epiphenomena.

Furthermore, Gould (1977, p. 379) claimed that the "... tradition of excellence in descriptive morphology is combined with a general avoidance of quantification,

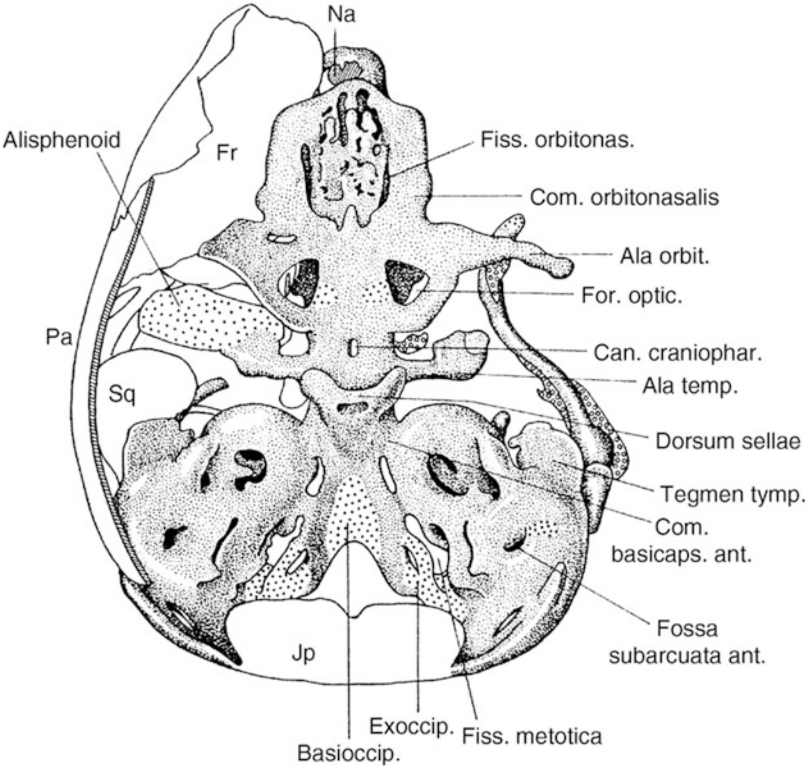

Fig. 2 Dorsal aspect of a fetal cranial model of *Pan troglodytes*. Crown-rump length: 71 mm. Not to scale (Modified from Starck and Kummer 1962)

and this may have hindered a full assessment." He might have overlooked an essential part of Starck and Kummer's (1962, p. 213) paper because "these findings can be characterized as quantitative. . .": (1) different relative sizes of the neurocranium and auditory capsule, (2) tegmen tympani, (3) frontal nasal region, (4) canaliculus chordae tympanic posterior, (5) commissura orbitonasalis, and others. Gould (1977, p. 384), however, did not fall into the Bolkian trap of an all-or-nothing law. Instead, he argued that "most of the classic 'exceptions' to human paedomorphosis are really consequences of retarded development," which Gould described as being the central phenomenon of our heterochronic evolution. Yet his ideas represent an analytic continuation of the Bolkian hypothesis.

Starck and Kummer (1962) did not exclude retardation (as in the commissura orbitonasalis) as an important factor of human development, but they emphasized that accelerations (e.g., the earlier closing of the intermaxillary suture in *Homo*) as well as deviations (e.g., the basicranium) should influence specific developmental processes. Starck's (1962, p. 23) summary revealed that the principles of human evolution cannot be understood through Bolk's hypothesis: important structures of the skull, very often taken as a result of fetalization, are indeed progressive compared with the pongid skull. It is emphasized that the bending of the skull base in man and apes is absolutely different, caused by different morphological structures. Identity of causal factors is not established, if we find external similarities, such as the same size of angles, of relative measurements or indices. This may happen by addition of completely different components.

This statement seems not to be a *furor teutonicus* but rather a well-balanced point of view. Hence, morphometrics might work, but the comparison of morphological details must occur in a correct manner. How do contemporary anthropologists interpret morphological changes of this important cranial region?

Developmental Aspects Concerning the Evolution of the Human Cranial Base

The cranial base represents the oldest component of the vertebrate skull (De Beer 1985). Thus this "conservative" structure is profoundly important in reflecting man's phylogenetic history and comparing primates to reveal essential aspects of human evolution. The keystone of the primate skull is definitely the basicranium. Several regions, such as the upper airway, the brain, and other parts, impinge upon one another here and consequently interact during ontogeny (Moss et al. 1982; Dean and Wood 1984; Lieberman et al. 2000). Biomechanically, the cranial base supplies a platform on which the brain develops and around which the face grows. The cranial base also forms a bridge connecting the cranium with the rest of the corpus: providing conduits for all circulatory and vital neural connections, articulating with the mandible and the vertebral column, forming the roof of the nasopharynx, and connecting the sense organs in the skull. Lieberman et al. (2000, p. 120) stated that "the shape of the cranial base is therefore a multifactorial product of numerous phylogenetic, developmental, and functional interactions."

Scientists are confronted with the problem of complicated circumstances in studying this truly important region. It is not only complexity that matters but also problematic ways of measuring. Furthermore, the fragmentary nature of fossil remains causes major difficulties. Novel analytical techniques, however, have helped to engross our thoughts over the past years. Different hypotheses exist that deal with ontogenetic spatial processes and their phylogenetic implications. I mainly follow Jeffery (2003) in reviewing some of the most popular versions. The *general spatial-packing hypothesis* states that the modern human basicranium is caused by a short cranial base and an enlarged brain. Ross and Ravosa (1993) and Ross and Henneberg (1995) revealed significant positive correlations between increases of relative brain size and cranial base flexion across adult primate taxa: correlation of increasing relative brain size with (1) a coronal reorientation of the petrous bones across extant primates (Spoor 1997), (2) a cranial base flexion using different measurements and landmarks (Spoor 1997; McCarthy 2001), and (3) a cranial base flexion after controlling for the influence of phylogenetic correlations (Lieberman et al. 2000). Enlow and colleagues (Enlow and Hunter 1968; Enlow 1976, 1990) also attempted to demonstrate a determination of cranial base flexion through increases in relative brain size during primate development. Jeffery and Spoor (2002) could not verify these authors' arguments. They analyzed specimens from 10 to 29 weeks of gestation and documented that petrous orientation remains independent of significant increases in relative brain size. Furthermore, a retroflexion of the midline cranial base with relative endocranial size increases has been suggested. This observation contradicts the predicted flexion pattern.

The *infratentorial spatial-packing hypothesis* has been revitalized by Dean (1988), who argued that having coronally oriented petrous bones and a highly flexed basicranium poses the spatial problem of fitting an enlarged cerebellum on a short posterior cranial base. Jeffery and Spoor (2002) showed that ontogenetic data, collected during the second and early third trimesters of human prenatal development, do not support Dean's (1988) claim. They indicate that the petrous orientation and cranial base angulation do not correlate with increases in infratentorial volume relative to posterior cranial base length.

The influence on skull form of patterns of brain growth is addressed by two interesting models. Hofer (1969) and Lieberman et al. (2000) favored the *brain shape hypothesis*, while Ross and Henneberg (1995), Chklovskii et al. (2002), and Sporns et al. (2002) supported a *neural-wiring hypothesis*. These ideas have in common a suggested necessary change in brain topography to maximize cognitive efficiency by reducing neural-wiring lengths. The resulting spatial changes produce a petrous reorientation and cranial base flexion. Distinct volumetric scaling trajectories can be detected across adult extant primates for different regions of the brain (Stephan et al. 1981, 1984; Frahm et al. 1982, 1998; Baron et al. 1987, 1990). Dean and Wood (1984) and Strait (1999) further demonstrated an association of those trends with interspecific variations in basicranial angulation. Lieberman et al. (2000) also confirmed a significant correlation of cranial base flexion with increases of cerebral volume over brainstem volume.

Moss et al. (1956) suggested that brain topography is shaped by differential encephalization patterns which lead to developmental changes in posterior cranial fossa morphology.

A few studies (Guihard-Costa and Larroche 1990, 1992; Jeffery 2002) on the human fetal brain showed greater increases in expansion of the supratentorial portion (containing the cerebrum) compared to the infratentorial portion (consisting of cerebellum and brainstem). However, the independence of human cranial base angulation and petrous orientation of changes from the volumetric proportions of the brain between the ages of 10 and 29 weeks gestation are corroborated by Jeffery and Spoor (2002).

Jeffery (2003) tested the key hypotheses by imaging fetal samples of *Alouatta caraya* and *Macaca nemestrina* using high-resolution MRI. He noted marked increases in brain size, especially "disproportionate increases in the size of the cerebrum" (p. 281), disproportionate growth of the anterior midline basicranium compared with the posterior midline basicranium, coronal reorientation of the petrous bones, and cranial base retroflexion. Contrary to the spatial-packing hypotheses, increase in relative brain size is not accompanied by flexion of the midline basicranium. Retroflexion is documented for the cranial base in both taxa. There is also little evidence supporting the spatial-packing hypothesis for the fetal period of the howler monkey and macaque due to significant and "seemingly" consistent associations with petrous orientation arise based on background covariations with somatic growth. Jeffery (2003) therefore suggested that laryngeal size might be the reason for basicranial retroflexion. He finally compared it to human fetuses and concluded that the establishment of notable interspecific differences in the basicranium occurs much earlier than in the phase he studied.

Craniofacial growth patterns have been studied by several scientists (Giles 1956; Shea 1983, 1985a, b; Jungers and Hartman 1988; Ravosa 1991, 1992; Zumpano and Richtsmeier 2003; Cobb and O'Higgins 2004; Mitteroecker et al. 2004). Lieberman et al. (2000) provided a comprehensive review of primate cranial base studies. As Zumpano and Richtsmeier (2003) pointed out, many previous studies documented postnatal growth processes, usually beginning with growth during the juvenile period. The infant growth period has been incorporated by Ravosa (1992), Richtsmeier et al. (1993), or Shea (1983), while Zumpano and Sirianni (1994) compared fetal to postnatal craniofacial growth patterns. Collections of fetal primates very often do not contain representative specimens (Zumpano and Richtsmeier 2003, p. 340). Yet it is desirable to attempt an integration of these stages since only a completely documented ontogeny delivers deeper insight to reveal whether heterochronic processes are responsible for the modifications that have occurred between human and nonhuman primates.

Zumpano and Richtsmeier (2003) investigated, for the first time, growth-related shape changes in the fetal craniofacial region of humans and pigtailed macaques (*M. nemestrina*), using three-dimensional comparative analysis via cross-sectional samples of CT image data. As they emphasized, a long tradition of studies concentrated on examining the sites of growth of the cranial base, the sites of cranial base flexure, and the determination of the cranial base angle (Bjork 1955; Ford 1956; Dubrul and Laskin 1961; Houpt 1970; Lavelle 1974; Bosma 1976; Lestrel and Moore 1978; Moore 1978; Sirianni and Van Ness 1978; Sirianni and Newell-Morris 1980; Ross and Ravosa 1993; Ross and Henneberg 1995; Zumpano and Richtsmeier 2003). Zumpano and Richtsmeier (2003) showed that decreases in human cranial base length are achieved through the differential growth of posterior and anterior elements. The length of the posterior cranial base decreases, while increases occur in the length of the anterior cranial base. They further argue that a cranial base angle decrease may lead to a total reduction in cranial base length in human fetuses. At a comparable stage, the fetal macaque cranial base does not show a corresponding reduction (increased basicranial flexion). The associated distinctiveness of the differences in midfacial growth and the progression of prenatal cranial base flexion are said to be factors separating these two species. Zumpano and Richtsmeier (2003) also contradicted Bjork (1955) and Ford (1956) in noting a basicranial flexion – not a constant angle – during the fetal period. They further support Lestrel and Moore (1978), and Sirianni and Newell-Morris (1980) are also supported in assuming a constant macaque cranial base angle during fetal growth, although they report a lesser angle (153°). The human anterior cranial base undergoes more relative growth than the macaque anterior cranial base. For the posterior cranial base, no significant growth differences between these two species are observed. Zumpano and Richtsmeier (2003) speculated that the increases in relative length of the anterior cranial base in humans may reflect the faster rate of growth of the frontal lobes of the cerebral cortex in humans relative to macaques (Enlow and Hunter 1968; Moss and Salentijn 1969; Moss 1973; Sirianni and Newell-Morris 1980) and conclude, based on their own observations and the studies of Anemone and Watts (1992) and Swindler (1985), that midface differences between humans and macaques reflect a delayed rate of maturation of the human deciduous dentition *or* an accelerated rate of development. In a tabula rasa manner, Zumpano and Richtsmeier (2003) supported earlier investigations in suggesting the occurrence of shape changes within the fetal craniofacial complex during the last trimester of fetal growth (Grausz 1991; Plavcan and German 1995) rather than assuming an isometric growth process that is, e.g., characterized by size increase without corresponding shape change (Mestre 1959; Houpt 1970; Kvinnsland 1971a, b; Lavelle 1974; Moore and Phillips 1980; Sirianni and Newell-Morris 1980; quoted from Zumpano and Richtsmeier 2003). Zumpano and Richtsmeier (2003, p. 349) finally concluded that "fetal macaques and humans do not share a common pattern of relative growth of the craniofacial complex, both species undergo increases in mediolateral dimensions (widening) of the skull and increases in palatal and anterior cranial base length."

One of the ultimate goals in paleoanthropology is to reveal the precise relationship of humans to the great apes, our closest living relatives. Morphological data favor the monophyly of the African great apes, while molecular biology unites humans and chimpanzees (Mann and Weiss 1996; Ruvolo 1997; Enard et al. 2002; Kaessmann and Pääbo 2002). Wildman et al. (2003) even placed chimpanzees within *Homo* based on molecular data. Pääbo (1999) emphasized the importance of investigating a few genes that are responsible for specific effects during ontogeny (or in adulthood) instead of concentrating on chromosomal rearrangements or the accumulation of point mutations. Hence, Mitteroecker et al. (2004, p. 680) stated that "as it is difficult to study gene expression on a molecular level for the whole organism, we confine ourselves to the study of the morphological effects of gene expression during ontogeny." They therefore created a shape space where each specimen (i.e., its landmark configuration) is represented by a single point. In this context, an ontogenetic trajectory corresponds to the ontogenetic sequence which belongs to one species within this space. As Klingenberg (1998) or O'Higgins (2000a, b) showed, geometric contrasts among ontogenetic shape trajectories distinguish the development of different species. Geometric morphometrics is a promising and complex method of collecting and interpreting data based on morphological patterns (Bookstein 1991; Marcus 1996; Dryden and Mardia 1998; Slice 2005).

Some hominid craniofacial growth studies, applying geometric morphometrics, found more or less parallel trajectories from dental stage I (which corresponds to the first permanent molar) to adulthood (Ponce de León and Zollikofer 2001; Penin et al. 2002). The development of hominid cranial morphology consequently diverges from that of the other apes in an early postnatal or prenatal stage. However, O'Higgins (2000a; O'Higgins et al. 2001) confirmed Richtsmeier et al.'s (1993) assumption of related species subsequently diverging after a similar period of early development. In a comprehensive study, Mitteroecker et al. (2004) measured landmarks and semi-landmarks in relevant specimens following a few days after birth to reveal essential insights into hominid ontogeny. Several principal patterns can be deduced from the set of ontogenetic trajectories. The authors tested three specific hypotheses: (1) “pure heterochrony” of human cranial growth relative to *Pan* is a valid interpretation if the ontogenetic trajectories are identical in shape space, (2) the divergence of human ontogeny corresponds to a similar developmental stage at which the great apes diverge among themselves, and (3) an early divergence of trajectories from common ontogeny could elucidate the considerable morphological differences between humans and great apes because early modifications in development explain drastic transformations of the adult form (Richardson 1999). Studying 206 adult and 62 subadult crania of *Homo sapiens*, *Pan paniscus*, *P. troglodytes*, *Gorilla gorilla*, and *Pongo pygmaeus*, Mitteroecker et al. (2004) collected three-dimensional coordinates of 41 homologous ectocranial anatomical landmarks on the face and cranial base. They demonstrated the expected pattern whereby the youngest specimens are much more similar than the adults (von Baer’s omnipresent discovery). Already at birth, human craniofacial morphology differs markedly from apes (p. 692) “in accord with previous studies based on more traditional methods” (Starck and Kummer 1962; Dean and Wood 1984). The first hypothesis, in contrast, can be rejected because there is no sharing of a common ontogenetic trajectory. Penin et al. (2002) tried to revitalize the “neotenic theory” sensu Gould (1977, p. 365). They do not, however, support a “general, temporal retardation of development” but rather stress that “all the bipedal traits studied, whether in the skull (basicranium) or postcranium (pelvis and femur, see above), do not result from neotenic processes but rather from structural traits” (p. 61).

Additionally, the second hypothesis is falsified, and the third hypothesis is supported, by an earlier divergence of the human growth trajectory from the common hominid allometry (Mitteroecker et al. 2004, p. 692). The African apes also do not seem to be pure allometric variants of one single type. Mitteroecker et al. thus concluded (p. 694) that “pure heterochrony does not sufficiently explain human craniofacial morphology nor the differences among the great apes.” McBratney-Owen and Lieberman (2003) also provide insight into the postnatal ontogeny of facial position in *H. sapiens* and *P. troglodytes* by emphasizing that the ontogenetic integration of complex phenotypes, such as the face, occurs on multiple levels of development, and they further speculate about the effectiveness of ontogenetic analyses for testing hypotheses about natural selection.

Ackermann (2005) investigated similarities in cranial covariation patterns by obtaining measurements from 677 crania of adult and nonadult African apes and sub-Saharan humans to locate underlying developmental and functional causes for the patterning. Defining the points of divergence of the covariation patterns can offer insights into the action of selection on development. Ackermann’s work shows that patterns of integration are similar (not identical) among adult African apes and sub-Saharan humans. Ontogeny documents a sharing of patterns, with each species showing contributions to total integration from the oral region as well as from the zygomatic and to a lesser extent the nasal regions. However, she documented important differences between apes and humans, stating:

"In particular, the lower overall integration within and lack of covariance structure similarity among adjacent ontogenetic stages in early human ontogeny differs from what we see in the other apes. It is not entirely clear why this might be so, although it indicates that selection was working in this lineage – either on humans or the apes – to distinguish them not only in morphology, but in variation patterning" (p. 195).

Quo Vadis? Developmental Aspects Concerning the Evolution of Bipedalism

I have already mentioned Bolk's (1926, p. 6) interesting ideas concerning human bipedalism "… since form became human the posture became upright" (my translation). Summarizing his growth studies on primates, Schultz (1924, p. 163) asserted that "man in some respects is less specialized and has hence remained phylogenetically as well as ontogenetically more original and 'primitive' than various other primates."

Structural and mechanical aspects of the locomotion of primates play a considerable role in many discussions of human evolution (Preuschoft 1971; Schaffler et al. 1985; Demes and Jungers 1993; Connour et al. 2000; Ruff 2002; see also Senut, Volume III). Schultz (1953) analyzed over 350 limb bone circumferences and related the results to locomotion. The evolution of bipedal walking has, naturally enough, inspired scientists to associate locomotor mode with the relative lengths of the forelimb and hindlimb bones (Schultz 1937; Napier and Napier 1967; Jungers 1982). Changes within the hominin lineage in the relative size of the upper and lower limb bones are indications of our transition to bipedality (McHenry 1978; Johanson et al. 1982; Wolpoff 1983; Hartwig-Scherer and Martin 1991; McHenry and Berger 1998; Asfaw et al. 1999; Richmond et al. 2002; Ward 2002).

A few French scientists (Berge 1998) have tried to integrate heterochronic processes into analyses of morphological changes during hominid evolution. These works have concentrated on such classic anthropological topics as the anatomy of the pelvis. Berge (1998, p. 443) emphasized separating the debate on neoteny by negating the idea "that identical heterochronic processes occur in skulls and postcranial skeletons, although we know that the growth of cranial and long bones differs in time, rhythm and velocity." She studied the morphology of two adult pelves and a juvenile hip bone of australopiths, 60 juvenile and adult pelves of modern humans, and 150 juvenile and adult pelves of African apes. The results confirmed a marked difference of the pelvic growth pattern in African apes and humans as reflected in multivariate results, ontogenetic allometries, and growth curves. Two conclusions emerged: (1) a comparison of modern humans to juvenile and adult australopithecines reveals that a unique feature of *Homo* seems to be a prolonged growth in length of hindlimb and pelvis after sexual maturity, while pelvic growth of *Australopithecus* was probably closer to that of apes than to that of humans and that some pelvis traits of adult *Australopithecus* resemble those of neonate *Homo*. Furthermore, (2) at the time of human birth, the appearance of the acetabulo-cristal buttress and the cristal tubercle allows the addition of features, such as the attainment of a proportionally narrower pelvis, with more sagittally positioned iliac blades. In early childhood (as bipedalism is practiced), pelvic orientation and proportions change progressively, while other changes in proportions occur later with the adolescent growth spurt. Neonate *Homo* and adult *Australopithecus* show similar patterns concerning the position of the acetabulo-cristal buttress. This could suggest a later displacement during human evolution. Berge (1998) further documented a progressive displacement of the acetabulo-cristal buttress on the ilium occurring during human growth (from neonate to adult) and hominid evolution (from *Australopithecus* to *H. sapiens*). She finally suggested that the evolution of pelvic morphology in hominids is based on a threefold process – predisplacement, acceleration, and time hypermorphosis – and she rejected pure fetalization (p. 457) by stating that "the present study demonstrates clearly that the concept of neoteny is irrelevant for the pelvis. The study rather implies an accelerated evolutionary process than a retarded one."

Ruff (2003) examined the human development of femoral to humeral proportions using a longitudinal sample of 20 individuals measured radiographically at semiannual or annual intervals from 6 months of age to late adolescence and also included anthropometric data such as body weights or muscle breadths. A series of limb bone length proportion studies included ontogenetic data (Lumer 1939; Schultz 1973; Jungers and Fleagle 1980; Buschang 1982; Shea 1983; Jungers and Susman 1984). Ruff (2003) focused on other limb bone dimensions. He compared his results with a cross-sectional ontogenetic sample of 30 baboons. The results document that femoral/humeral length proportions, which are already close to those of adults, are present in human infants, while characteristically femoral/humeral diaphyseal strength proportions only develop after the adoption of bipedalism (at about 1 year of age). Between the age of one and three, a rapid increase in femoral/humeral strength occurs, and this is followed by a slow increase until mid-late adolescence (when adult proportions are reached). The femoral/humeral length ratio proportions slightly increase throughout growth. There is no apparent growth trajectory change at the initiation of walking and a small decline in late adolescence based on a later humeral growth in length. Also in early childhood, a sex difference in femoral/humeral strength proportions (but not length proportions) develops. Ruff (2003) therefore concluded that they must be largely independent of growth trajectories in strength and length proportions. Baboons (used as a baseline) show contrasting patterns of growth: much smaller age changes in proportions and particularly strength proportions. He therefore stated (p. 342): "Comparisons with an ontogenetic baboon sample highlight the specific nature of the human developmental pattern."

Returning to Adolph H. Schultz, we have an excellent example of a convert. In his youth, Schultz was stimulated by the neoteny hypothesis (see earlier). Following several studies (1953, 1973) although, he rejected Bolk's idea and the theory of man's neoteny.

Heterochrony in Human Evolution: A Compilation

Repetitio est mater studiorum or as Schwartz (1999, p. ix) commented: ". . . it would be foolhardy to cling unreservedly to a particular set of models and hypotheses without at least occasionally questioning their very bases." In *Sudden Origins*, Schwartz reconsidered and discussed inter alia the different interpretation of the Taung child. While Raymond Dart was influenced by ideas of neoteny and concluded that his fossil

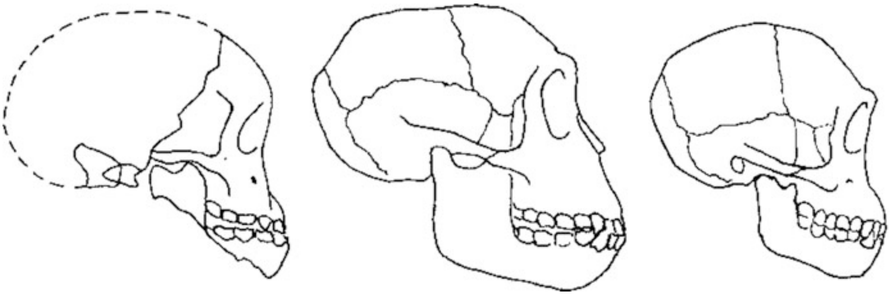

Fig. 3 The Taung child (*left*), compared to the skulls of comparably aged gorilla (*middle*) and chimpanzee (*right*). Dart's desire was to show that the apes had begun to grow away from the juvenile state. The Taung specimen has no brow ridges, small jaws, and a very large brain (Modified from Schwartz 1999, drawing by T. D. Smith, © J. H. Schwartz)

occupied a missing link position, Sir Arthur Keith drew a totally different conclusion and defined the Taung individual as an ape. Ironically, Keith's results were also based on a developmental and even a neotenic chain of ideas (Fig. 3).

Furthermore, Schwartz (1999) critically reviewed the suggestions of the Australian anthropologist Andrew Arthur Abbie, who equated neoteny and paedomorphism, and portrayed *H. sapiens* due to its long legs and a highly arched nose as gerontomorphic (more differentiated from a fetal standard), although he generally described our species as paedomorphic (little differences from a fetal standard). Abbie absorbed the heterochronic perspective but failed to sustain the argument that human morphological variability is not fixed to a limit and that any combination of features can be incorporated in the same individual.

Gould (1977, 1991, p. 2) called attention to the difference between Haeckel's heterochrony, which describes the *pathway of development in an organ relative to the pathways of other organs in the same animal*, and current usage, which defines it as "the course of a trait relative to the ontogeny of the same trait in an ancestor (or related form)." Jena's most famous zoologist was not really interested in elucidating evolutionary mechanisms as a method to explain the patterns of character states. He was rather interested in reconstructing natural history by applying biogenetic laws. Sir Gavin de Beer (1930) opened up new vistas by modifying Haeckel's concept: any change in the timing of a character is compared to the same feature in an ancestor. This established the study of heterochrony within the modern synthesis (Gould 1991).

McNamara (2002, p. 1) defined heterochrony essentially as "change to the timing and rate of development" which produces two major effects: *paedomorphosis* (if there is less growth during ontogeny, the descendant adult will resemble the juvenile condition of the ancestor) and *peramorphosis* (where the descendant undergoes greater development). Three different processes generate paedomorphosis and peramorphosis, respectively: (1) progenesis (prematurely truncated duration of growth in the descendant), neoteny (a lesser growth rate in the descendant than in the ancestor), and postdisplacement (delayed onset of growth) and (2) hypermorphosis (extension of duration of growth in the descendant), acceleration (an increase of growth rate in the descendant), and predisplacement (earlier onset of growth in the descendant). The whole organism can only be affected by progenesis and hypermorphosis, while the remaining aspects affect certain traits of the organism. McNamara (2002) further stated that peramorphosis and paedomorphosis are the products of varied processes rather than being processes in themselves. Hypermorphosis (extensions of the end of growth) and progenesis (contractions of the end of growth) are considered within a global context, “based on changes to the time of onset of sexual maturity and cessation of somatic growth, with the two frequently coinciding” (McNamara 2002, p. 105).

Different views have emerged on how large a role neoteny plays. While Gould (1977), Antón and Leigh (1998), and Montagu (1989) supported true paedomorphosis (neoteny), Shea (1988, 1989, 1992), McKinney and McNamara (1991), and McNamara (1997) favored some kind of hypermorphosis in time. Bogin (1997) suggested a new developmental stage in between (no heterochrony); Alba (2002) on the other hand characterized paedomorphosis and peramorphosis as *interpretative*, not descriptive, terms. He emphasized the importance of modifying conventional clock models based on meaningful variables. Alba (2002) called for a double standardization (initial and final developmental stages) of ontogenetic trajectories and suggests a “complete” model including absolute age (at homologous developmental stages), shape, size, and behavior. As he admitted, this is not an easy undertaking.

McKinney and McNamara (1991) have indicated that, during ontogeny, contractions and extensions can occur at transitions between particular life-history stages and that local growth fields can also be modified. The reality that heterochrony may operate at *any time during ontogeny* (from the point of fertilization until the cessation of growth) has been blurred by the comparison of the cessation of a descendant’s growth with the ancestral condition (McNamara 1983; McKinney and McNamara 1991; Maier 1999). Mammals, for example, are characterized by embryonic and postembryonic (infantile, juvenile, adolescent, and adult) growth phases. In his thought experiments, McNamara (2002) showed how some authors have described paedomorphosis where it was nonexistent. Sequential hypermorphosis (defined by him in 1983 as *terminal hypermorphosis*), for instance, also effects the offset of growth and therefore implicates greater development within each growth stage based on “scaling effects and probable increase in size, either of the part, or of the whole” (2002, p. 108). Hence, the descendant is compared to the ancestor in a relatively more juvenile state. Paedomorphosis, however, should be defined by *adult* characteristics.

What kind of consequences does sequential heterochrony have for our understanding of human evolution? The list of “general neoteny supporters” is long (I have already mentioned Bolk and Gould, but see also Montagu 1989; Wolpert 1991). Montagu’s (1989) favorite ancestor is a form very like the pygmy chimpanzee in order to compensate the incorrect assumption of Bolk that the hominid line has passed through an apelike stage such as the gorilla-orang type. Provided that human is “essentially neotenous,” hominid evolution would have produced an organism characterized by having a smaller body size, brain, and limbs

(Shea 1989; McKinney 1998). McNamara's (2002, p. 115) summary described hominid evolution as involving "a mixture of peramorphic and paedomorphic traits." Forty years back, Starck and Kummer (1962) had come to a similar conclusion via a totally different method.

Shea (2002, p. 95) applied his working hypothesis – size diversification occurs via predominant rate changes (rate hypomorphosis and hypermorphosis) rather than by time changes (time hypomorphosis and hypermorphosis) – to human evolution and concluded that: "Certainly, at present no emergent data support any genetic or developmental basis for a global or generalized neoteny." He accused Godfrey and Sutherland (1996) of revitalizing the idea that hominid evolution has predominantly involved a generalized neotenic transformation. This accusation is problematic in that Godfrey and Sutherland (1996, p. 40) freely admitted that "Gould's neoteny hypothesis for human evolution has been criticized on a number of grounds. The thesis of this paper is that both Gould and his critics overstated their cases: *Nothing that we have said should be construed as a defense of Gould's hypothesis*. Our intention is simply to reopen the dialogue, and to propose a framework for more precise testing of heterochronic hypotheses" (my emphasis).

In contrast, Hall (2002, p. 13) attacked the one-sided concentration on heterochrony as the only way to consider development and evolution by claiming that it "seemed that everyone could find evidence for heterochrony or at least justify use of the term to explain phenotypic changes in their favourite organism. Other mechanisms linking development and evolution were ignored or not sought." He emphasized the importance of heterotopy, the *spatial pendant* of heterochrony.

In summary, I give below some important terms and definitions (see also earlier) based on Minugh-Purvis and McNamaras' (2002) summary, to present a brief synopsis:

Acceleration	A heterochronic process that involves a faster rate of development in the descendant and also produces a peramorphic trait in the descendant
Deceleration	A slower rate of developmental events in the descendant. It produces a paedomorphic trait when expressed in the adult phenotype (syn. neoteny)
Hypermorphosis	Developmental events show a delayed cessation (or offset) in the descendant. Expressed in the adult phenotype, peramorphic traits are produced. Global hypermorphosis can be caused by late sexual maturation (terminal hypermorphosis). But hypermorphosis can also be caused by a delayed cessation in local growth fields
Isomorphosis	Peramorphosis followed by paedomorphosis (or vice versa). The descendant does not show any effective morphological changes. Unusual phenomenon of paedomorphosis
Neoteny	A slower rate of developmental events in the descendant, producing paedomorphic traits when expressed in the adult phenotype (syn. deceleration)
Paedomorphosis	The descendant adult retains subadult ancestral traits
Peramorphosis	The ancestral adult shows development of traits beyond the "usual" ancestral stage

(*continued*)

Progenesis	Developmental events show an early cessation in the descendant. Expressed in the adult phenotype, peramorphosis is produced (syn. time hypomorphosis)
Sequential heterochrony	Contraction or prolongation in the descendant relative to the ancestor of life-history stages or ontogenetic growth
Sequential hypermorphosis	Life-history stages or ontogenetic growth is prolonged in the descendant relative to the ancestor (syn. proportional growth proportion)

Tolkien's Hobbits Came True: *H. floresiensis* and Heterochrony

In his first chapter of his book *The Hobbit*, "An unexpected party," J. R. R. Tolkien described these creatures as wearing ". . . no shoes, because their feet grow natural leathery soles and thick warm brown hair like the stuff on their heads; have long clever brown fingers, good-natured faces,. . ." Furthermore, and more importantly, the author characterized them as "..little people, about half of our height" (Tolkien 2007, p. 4). *Homo floresiensis* was named for Pleistocene hominid remains on the Island of Flores (Indonesia) – these fossils in many ways represent the embodiment of Prof. Tolkien's fantastic creatures. However, for some researchers insular dwarfism by natural selection seems not to be a good explanation (e.g., Jacob et al. 2006). They prefer a pathologic scenario which reminds one of the interpretation of the Neanderthal enigma àla Rudolf Virchow.

The ontogeny-phylogeny nexus might serve as a plausible model for the evolution of *Homo floresiensis*. Kubo et al. (2013) analyzed the endocranial volume of LB1 via high-resolution micro-CT scans. They finally concluded that is mechanistically possible that the dwarfs from Flores evolved from early Indonesian *Homo erectus*. Mammals such as hippos have served as a model for brain size reduction in *Homo floresiensis* (Weston and Lister 2009). However, these studies have not deeply considered the role of ontogenetic processes. Van Heteren (2008) presented an interesting evo-devo approach by adapting the model of heterochrony – that, like the pygmy elephants of Cyprus, *H. floresiensis* might have stopped growth at an earlier age. Additionally, paedomorphic features might have developed "by making the rate of ossification increase" (p. 7).

In support of his hypothesis, Van Heteren (2008) adduced various cranial paedomorphic features such as the orbital index, the mandibular angle, the endocast, and the canine fossa. The dental index also supports his view of *H. floresiensis* as an interesting case of heterochrony. Furthermore, such postcranial adaptations as the humeral and tibial torsion or the brachial index may indicate neoteny. Although the detailed interpretation of these characteristics cannot be considered in this review, the Dutch tradition of considering ontogenetic interpretations when reconstructing phylogeny remains vivid.

As I have shown earlier, the general neoteny theory of human evolution seems not to be the correct general approach to exploring our ancestry. Yet for the interpretation of particular problems of paleoanthropology such as the hobbit phenomenon, ontogenetic studies nonetheless represent powerful tools for phylogenetic research.

Conclusions

Alberch (1982) rightly pointed to the importance of developmental constraints in evolutionary processes. It is nevertheless also important to emphasize the highly informative aspects of development (e.g., Britz and Bartsch 2003; Cracraft 2005; Alemseged et al. 2006; Brakefield 2006) – we should appreciate the synergistic effects. Considering paleoanthropology, Dullemeijer (1975, p. 86) predicted that "the fundamental idea can inspire many in their future research if the foetalization theory is reduced to the right proportions, ... It seems to open great perspectives for anthropology." Two years later, Gould (1977) responded to this challenge and inspired a whole generation of biologists.

Most studies overwhelmingly reject a general neoteny phenomenon in human evolution. The conclusion of man's domination by neoteny represents a pithecocentric perspective: a fruitful but wrong hypothesis. Sophisticated techniques, such as geometric morphometrics, and more embryological data indeed improve the quality of the data sets but on the whole often verify traditional contributions. Gould's (1977) brilliant *forte*, however, was primarily to break down the language barrier and to revitalize the topics of ontogeny *and*Phylogeny. *Summa summarum*, I would like to conclude with Dullemeijer's (1975, p. 84) take-home message – not only in the figurative sense – by stating: "*Homo sapiens* has its own face."

Cross-References

- ▶ Fossil Record of Miocene Hominoids
- ▶ Fossil Record of the Primates From the Paleocene to the Oligocene
- ▶ General Principles of Evolutionary Morphology
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ *Homo floresiensis*
- ▶ Modeling the Past: The Primatological Approach
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of Speech and Language
- ▶ Virtual Anthropology and Biomechanics

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Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms

Michael Ohl

Contents

Abstract

Taxonomy deals with the naming and classification of organisms and is an integrative part of biological systematics, the science of biodiversity. The information provided by taxonomic research is a fundamental basis for all fields of biology. Current taxonomy focuses on multicharacter integrative approaches, considering all potentially useful sources of information provided by the various fields of biology. The resulting supraspecific classification should be based on the genealogy of organisms, that is, on a phylogenetic analysis, to be objectively testable. However, for pragmatical reasons, a classification based on overall similarity and diagnostically relevant characters might be a heuristically important step in taxonomy and should be perceived as an approximation to a

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M. Ohl (✉)
Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Museum für Naturkunde, Berlin, Germany
e-mail: michael.ohl@mfn-berlin.de

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classification tested by phylogenetic methods. The nested levels in a classification of organisms are usually not only named but also ranked, that is, a set of hierarchical terms, like *genus*, *family*, and *class*, is applied to reflect the hierarchical structure of the classification. Assigning these so-called Linnaean categories to a classification is (1) a voluntary action to make a classification notionally more easy to access and (2) a linguistic activity that is done subsequent to obtaining the scientific results of the systematic analysis.

Introduction

Taxonomy, the science and method of naming organisms, is a fundamental basis for all biological science and its application (Sluys 2013). The primary task of taxonomy is to describe, establish, and give an account of the order that is an inherent property of biological diversity. The order of names provided by taxonomy is arranged as a hierarchical classification, which is considered to portray the hierarchy of species and more inclusive taxa as a result of the continuous chain of species splittings in the evolutionary history of life on earth. Generalizations on organisms as a basic principle in biology are only possible if the infinite number of items in science is classified. Statements about the overwhelming diversity of nature would be impossible without methods for bringing order to this diversity. The world's biota is a vast library of information concerning any aspect of life, and taxonomy is the cataloguing system that everybody must use to access its information. All kinds of biological science and applications link their specific data to species names and use these names for effective communication. As Longino (1993, p. 85) has paraphrased, "… taxonomy is the raw material from which hypotheses of phylogeny are derived." All kinds of comparative biology rely on sound phylogenetic hypotheses, and the reliability of a phylogenetic hypothesis immediately depends on the reliability of the underlying taxonomic data. Moreover, society has an increasing need for reliable taxonomic information in order to allow to manage and understand the world's biodiversity (Wheeler et al. 2004; Costello et al. 2013). Until recently, taxonomy was confronted with what Godfray (2002, p. 17) called a new bioinformatics crisis, evidenced "by a lack of prestige and resources that is crippling the continuing cataloguing of biodiversity." Current biological taxonomy quite successfully adopts methods, data structure, and other demands of techniques and theories invented by new entrants to the biological sciences such as the fields of molecular biology (e.g., DNA barcoding; see De Salle et al. 2005). However, all other useful sources of information are simultaneously gathered in modern taxonomy, and this multicharacter integrative approach has been called *integrative taxonomy* (Dayrat 2005; Wheeler 2005; Padial et al. 2010). It allows taxonomists to create new common visions to meet changing demands of a changing global view on global biodiversity and the threats to it (Wheeler and Valdecasas 2005; Wheeler 2008; Polaszek 2010; Wheeler et al. 2012).

Definitions

Inconsistent terminology is a barrier to communication, results in confusion and misunderstanding, and prevents effective science. The variation in definitions for “taxonomy,” “systematics,” “classification,” and related or derived terms is as complex as it is contradictory. The major problem with these obviously closely allied terms is to differentiate them from each other, and many authors treat them more or less as synonyms, either intentionally or intuitively. In a recent textbook on biological systematics, Schuh (2000) implicitly equated systematics, classification, and taxonomy, when he defined systematics as “the science of biological classification.” The opposite view is held by Hawksworth and Bisby (1988, p. 10), who suggested restricting taxonomy to “taxonomic information systems (classification, nomenclature, descriptions, identification aids)” and defining systematics to include “taxonomy in the above restricted sense together with analyses of variation, of phylogeny, evolutionary processes, etc.”

Probably, most current scientists would agree that the most appropriate name for the scientific area composed of taxonomy, systematics, classification, and all of their respective concepts, theories, and methods is “biological systematics,” or systematics in short.

What are the basic units of systematics? Systematics is not concerned with individual organisms, although these are always studied by systematists as representatives of species or other supraspecific groupings. The simplest and most descriptive statement would be that systematics deals with taxa. What then is a *taxon* (plural, taxa)? Simpson (1961, p. 19) defined it as “a group of real organisms recognized as a formal unit at any level of a hierarchic classification.” This definition recognizes groups of organisms as taxa only if they are already formally classified, which is not always necessary or wanted. Newly discovered groups, hypothetical groups that still await confirmation, putatively artificial groups that are still disputed, and many others do not qualify as taxa under Simpson’s definition. In the field of phylogenetic systematics or cladistics, the taxon definition is often narrowed even further to monophyletic groups of organisms (Sudhaus and Rehfeld 1992; Mayr and Bock 2002). The final objective of systematics is indeed to include monophyletic groups only, but for a wide variety of reasons, this goal can hardly be achieved right away. Hypotheses on monophyly are created and rejected, groups prove to be nonmonophyletic but are still being discussed, and putatively monophyletic groups are still of unknown position within a certain higher lineage. Other problematic cases are fossil stem groups, like Australopithecinae, which are obviously paraphyletic with respect to Hominidae but can be treated as a heuristically important grouping in paleoanthropology. All these groupings are best referred to by a generalized term, and taxon is the most appropriate one. Hence, a definition of the term taxon might be: “A taxon is a group of organisms that can be differentiated from other groups of organisms, and that can be described and named.” Other terms to replace the term taxon have been proposed that are considered to carry specific connotations to reflect a specific framework for which they have been proposed.

Terminal taxon, as used in cladistics, and *operational taxonomic unit* (OTU), proposed by the phenetic school of systematics, are two prominent examples that have been suggested to designate the units of systematics without reference to a particular rank or phylogenetic position. However, the term taxon, as here defined, is sufficient to refer to ranked and unranked groups of organisms.

Biological systematics in fact deals with taxa, that is, biological populations, species, and higher taxa. However, systematics is concerned not only with the taxa themselves and their description and characterization but also with their origin, development, and other kinds of interrelationships. The fundamental and underlying concept of systematics is evolution, and Huxley (1940a, b) regarded systematics as "detecting evolution at work." Simpson's (1961, p. 7) classical definition of biological systematics (or just systematics) is still adequate: "Systematics is the scientific study of kinds and diversity of organisms and of any and all relationships among them." This definition was subsequently simplified to include the modern term "biodiversity," e.g., Mayr and Ashlock (1991) and Sudhaus and Rehfeld (1992, p. 11): "Systematics is the science of the diversity of organisms."

Another term that plays an important role in biodiversity research is taxonomy. Taxonomy is not easy to differentiate from systematics, and it has been frequently intermingled with systematics. If separated, taxonomy usually refers to what Hawksworth and Bisby (1988, p. 10) called "taxonomic information systems," i.e., naming of taxa, nomenclature, descriptions, and identification aids, whereas systematics is widely understood in a general sense of including taxonomy and the analysis of phylogenetic relationships, speciation processes, variation, and others. Since under any definition the terms taxonomy and systematics are closely associated, many authors have simply synonymized them because they consider their separation not to be feasible. The development of a concise methodology and theory of phylogenetic systematics in the last decades has considerably influenced the practice of modern taxonomy. Taxonomy, as understood here, might be treated as a field of systematics, with specific methods, theories, conventions, and terminologies that are different from other systematic fields (Will and Rubinoff 2004). There is, of course, continuous, active transgression of the borders between taxonomy and other branches of systematics, such as phylogeny and biogeography, and the most desired taxonomic revisions are obviously those whose taxonomic decisions are tested by phylogenetic analysis. To summarize, an appropriate definition of taxonomy might be (modified from Winston 1999, p. 9):

> Taxonomy is the branch of biological systematics that is concerned with naming of organisms (according to a set of rules developed for the process), identification (referring specimens to previously named taxa), and classification (ordering taxa into an encaptic hierarchy based on perceived characters).

The set of rules that governs the formation and use of taxon names in zoology is provided by the *International Code of Zoological Nomenclature* (hereafter referred to as the *Code*), published by the *International Commission on Zoological Nomenclature* and currently in its fourth edition. The Code and its bearing on taxonomy will be briefly discussed later. The definition described earlier points out that a classification of organisms is based on perceived characters. Any organism consists of innumerable numbers of characters that can potentially be perceived by a biologist, but not all of them qualify as characters helpful in achieving a meaningful classification. The so-called phylogenetic systematics provides the objective framework for evaluating characters according to their meaning for the evolution of a taxon. The most reliable and testable classification is based on the results of a phylogenetic analysis, which tries to reconstruct the hierarchical structure of organisms as a result of the continuous sequence of speciation events in evolution. This should be the basic goal of all taxonomy. However, for different reasons, phylogenetic relatedness might (still) be unknown, and thus the set of perceived characters for establishing a sound classification might be selected intersubjectively by means of overall similarity and diagnostically relevant characters. A classification based on overall similarity might be a heuristically important step in biological systematics and should be perceived as an approximation to a classification based on phylogenetic hypotheses. In practice, such non- (or pre)phylogenetic classifications might stand for a long time, but they should be regarded as preliminary until tested by phylogenetic methods.

The previously mentioned definition of taxonomy implies that one of its main goals is a classification. As paraphrased by Schuh (2000, p. 15), a “classification represents the codification of the results of [bio]systematic studies.” A general definition of classification might be:

> A classification is a set of names that are ordered hierarchically and more and more inclusive. The hierarchy of names is considered to portray the hierarchy of organisms as the result of the evolutionary process.

Again, the hierarchy of organisms should preferably be recovered by means of phylogenetic methods but might be preliminarily but meaningfully approached by the criterion of overall similarity.

Some authors (Griffiths 1974; Wägele 2005) differentiate classification from *systematization* for fundamental reasons. The term classification originates from the term *class* as in use in the philosophical logic and means a group of objects that have a specific set of properties in common. Which property is selected as class-defining is purely subjective and arbitrary, and a classification based on this property is similarly subjective. Thus, a classification, as defined by Wägele and others, is considered to be a strictly conceptual system and is the product of an arbitrary, linguistic activity. In contrast, organisms are the product of the historical process of evolution, which is expressed as a continuous chain of speciation events during the history of life. The sequence of species splittings over millions of years has resulted in a hierarchical structure of the organisms that systematists achieve to *reconstruct*. Thus, this kind of hierarchy is conceptual as well, but it is considered to represent the hypothetically real sequence of speciation events in evolution. This process is called systematization by Wägele (2005). The conceptual representation of the mental order as achieved by the process of systematization is called a *phylogenetic system*. The difference between a classification and a systematization is of fundamental importance but is usually not considered in practical biological systematics. The term classification is used here for both ordering systems, which is in accord with the widely accepted understanding, but the resulting double meaning of classification and the respective subtle differences to systematization must be kept in mind.

A completed classification is a hierarchy of names that denote hypotheses on taxa. It is organized in a more and more inclusive terminological structure of a theoretically infinite number of levels. These levels may bear names, but many of them, particularly in fully resolved cladograms with vast numbers of levels, remain unnamed for practical reasons. After completing a classification and selecting an appropriate number of higher taxa to be named, the hierarchically organized set of named levels can be given relative ranks as individual designations. Such relative ranks are provided by *categories*, such as classes, families, and genera, and this system of categories is well known as the *Linnaean hierarchy* or the *Linnaean categories*. Although the meaning and the current status of the Linnaean categories will be discussed later in more detail, it should be stressed here that an assignment of Linnaean categories to the level of a classification is (1) a voluntary action in order to make a classification notionally more easy to access and (2) a linguistic activity that is done subsequent to obtaining the scientific results of the systematic analysis.

As has been demonstrated previously, names as linguistic elements are of crucial importance in biological systematics. Names serve as labels to relate to concepts and hypotheses about taxa and their evolution. Names should principally be unequivocal, universal, international, and perpetual. Due to the incommensurably large number of organisms on earth, not to speak of the immense numbers of theoretically possible higher taxa that all could, at least in principle, be named, the need for internationally binding regulations is obvious. The part of taxonomy that is concerned with assigning names to taxa is called *nomenclature*. The sets of regulations that govern the practical application of nomenclature are provided by the International Code of Zoological Nomenclature.

Taxonomy as a System of Ordering Data

Biologists deal with a remarkable diversity of items. For any scientific procedure in biology, it is of critical importance to differentiate and thus to compare these items. It is one of the intrinsic attributes of a comparative process to arrange the to-be-compared items according to specified properties, that is, to *classify* these items. Mayr (1995) differentiated four different kinds of classifications: (1) special purpose classifications (based on particular features of special importance in the context, e.g., ecologists may divide small mammals into soil dwellers and tree dwellers), (2) downward classification by logical division (starting with the entire animal kingdom, groups are defined on the basis of dichotomous splittings in two less inclusive groups, such as the warm-blooded and the cold-blooded animals, until the species level is reached), (3) upward or grouping classification (items are arranged in more and more inclusive groups according to observed characters), and finally, (4) Hennigian phylogenetic or cladistic system (grouping of species and higher taxa on the basis of common descent). With respect to their nature as ordering systems, the upward classification (3) and phylogenetic systematics (4) do not differ, because in both classifications, species are combined into higher taxa (ranked as genera), these higher taxa are combined into even more inclusive taxa, and so forth. However, phylogenetic systematics is a special kind of upward classification in permitting only one criterion as the basis for the classification, that is, common descent.

Five basic objectives of ordering systems can be differentiated in general and apply to biological systematics as well (Vane-Wright 2001; Mayr and Bock 2002): (1) discrimination (delimiting groups against other groups), (2) information storage and retrieval (the structure of classification systems, based on different criteria that are considered to be informative regarding the group, permits storage and retrieval of a large amount of information), (3) recognizing group affiliations (this is called identification and refers to the process of referring an organism to a previously described taxon, e.g., by the use of a dichotomous key), (4) inferences about not yet studied properties (it is a widely held prediction that many of the characters of a taxon studied will be similar or even identical to those of closely or immediately related taxa), and (5) to serve as a baseline in comparative studies (the validity of comparative studies in biology largely depends on the reliability of the preceding research by which the studied items were grouped). These are basic objectives of that part of biological systematics that focuses on the biological items themselves, i.e., organisms, species, and higher taxa. The scientific treatment of these items requires a scientific terminology to communicate, which is provided by biological nomenclature.

Taxonomy and Classification Without Phylogeny: An Outdated Remnant or a Practical Necessity?

There is an increasing shift in taxonomy toward modifying the directives on how to name organisms to reflect genealogical relationships. However, despite the fact that most systematists would agree that the hierarchical system of names in biology should be governed by phylogenetic hypotheses instead of by intuitive similarity, the increasing pressure of phylogenetic demands on the naming processes results in intrinsic conflicts in systematics. Phylogenetic analyses have not been conducted for most groups of organisms yet, and it is highly unlikely that many will be undertaken soon. Additionally, new species are rapidly discovered in large numbers, particularly among invertebrates. Since a taxonomic treatment of such new taxa, that is, formal descriptions in taxonomic revisions or even single taxon descriptions, is a prerequisite to any other scientific exploration, new taxa are more rapidly described and made available than phylogenetic hypotheses are worked out. The taxonomic treatment of certain taxa, such as those that are less known, newly discovered, and/or extraordinarily species-rich, is a fundamental first step that opens up the possibility of continuing with subsequent phylogenetic, genetic, behavioral, and other studies.

In practical taxonomy, it is often necessary or at least recommendable initially to leave a comprehensive revision or a phylogenetic reconstruction aside from research projects and the resulting publications. In principle, Mayr and Ashlock (1991, p. 347) are correct that "the isolated description of ... new species ..., divorced from revisional or monographic work, is the least desirable form of taxonomic publication." But Mayr and Ashlock correctly qualify their assertion themselves in stating that it does not hold "in well-known groups." A well-known group is usually a taxon which is not only well known in terms of scientific research but also which additionally receives extraordinary attention by both the scientific and the general public. It is thus not surprising that isolated descriptions of fossil and recent Primates and large mammals often make their way to the highest-ranked scientific journals (e.g., the description of *Homo floresiensis* by Brown et al. 2004). Obviously, the publicity that results from such publications can be a strong motivation for any scientist to publish a rather isolated description immediately rather than to invest more time to obtain more data for a more comprehensive publication, due to the current system of scientists being under considerable pressure to publish and to compete for limited research money and, finally, jobs.

There are several more potential reasons to conduct *descriptive taxonomy* (Godfray 2002), which may mutually affect each other in most cases. Examples are as follows: (1) it might be desirable to make a new discovery formally available for further studies, which can or should not be conducted at the time of discovery of the new taxon for varying reasons; (2) if a scientist has discovered a new species, and if he intends to describe it formally, this scientist might want to guarantee that the name of this taxon as proposed by him is the first formal description and, thus, has priority over any subsequent name. This might be considered as to imply a connotation of personal rather than true scientific motivation, similar to the argumentation as presented earlier. However, priority is a basic principle of zoological nomenclature, and although it is explicitly thought to be priority of publication without reference to the date of discovery, the publication date here serves as an objectifiable reference point. Hence, priority of publication just replaces the priority of discovery for practical reasons; (3) incomplete knowledge of data might prevent systematists for conducting a comprehensive revision or a cladistic analysis. This might be due to the lack of characters (e.g., in fossils or other incompletely preserved specimens) or material (e.g., modern techniques such as molecular systematics or scanning electron microscopy require fresh or specifically preserved material, but many rare but potentially informative species are known only from dry museum material, which cannot be fully examined).

Another topic concerns the role of biological systematics in the context of a global biodiversity assessment. The development of global species inventories is considered to be an urgent and vitally important task that is a primary step and fundamental activity for any kind of biodiversity research (Stork and Samways 1995; Purvis and Hector 2000; Wilson 2003). Although it seems to be clearly unrealistic to describe every species of organism on earth, not to speak of the monumental uncertainties as to how many species there are (Godfray 2002), any step toward a global inventory of selected “target taxa” should be achieved as soon as possible.

Phylogenies are inherently hypothetical, simply because they portray historical processes, which cannot be inferred directly. Hypotheses, however, can be of different quality. The reliability of a hypothesis largely depends on the quality of the underlying data, which involves numerous theoretical and methodological aspects. Among these aspects, the *completeness* of the data set is of crucial importance. Completeness of characters is an illusion, since each single organism theoretically consists of an infinite number of characters. Completeness of taxa is, at least in principle, possible. With regard to taxon sampling, the perfect systematic study would include all species of a given taxon, perhaps even both still living and extant. Practically, completeness of taxa is unlikely to be achieved in most groups, except perhaps for some exceptionally well-studied taxa such as birds. However, the reliability of a phylogenetic analysis increases with the increasing completeness of the taxon sampling. Conversely, gaps in the taxon coverage result in considerably less reliable phylogenetic hypotheses. In many cases, phylogenetic analysis should better wait for a more complete species inventory, which, particularly in taxa with many species or with a patchy distribution, can hardly be achieved in one step.

In summary, publications concerned with the taxonomy of a given group are most desirable if their classificational results are based on a comprehensive phylogenetic hypothesis. If at all possible, a systematist should try to interpret his taxonomic data with respect to the corresponding phylogeny rather than relying on an intuitive character evaluation as a basis for a classification. Incidentally, since the hierarchical structure of the organisms on earth is the result of a historically real, continuous sequence of species splittings, the hierarchy of organisms as reconstructed by phylogenetic methods is in the end the only objective base for a classification.

Zoological Nomenclature: Governing the Process of Naming

Biologists are considered with myriad items, and these items need to be named to communicate concepts and hypothesis about these items in the biological sciences. It is not only the millions of species that have to be named. The hierarchical structure of the biodiversity of species and the myriad supraspecific taxa result in an almost infinite number of items that in principle can be named. Since names should be unequivocal in an international perspective, the formation and practical handling of names of species and higher taxa obviously need internationally binding regulations. Nomenclature is the part of taxonomy that regulates how names are assigned to taxa, and the underlying set of formal rules of how nomenclature is applied in practical zoology is the International Code of Zoological Nomenclature.

Ranking Hierarchies: Capacity and Limits of Linnaean Categories

The Linnaean categories are terms that identify the hierarchical level in a classification. Examples for categories are *genus*, *family*, and *class*. A limited number of such categories date back to Carolus Linnaeus' publications in the eighteenth century, but the number of categories has increased continuously over time, the better to reflect increasingly complex classifications. The rise of phylogenetic methods in the last few decades has resulted in an increasing number of cladograms that depict complex, not directly linear relationships with a seemingly infinite number of potential levels. It is, thus, not surprising that systematists face a myriad practical problems when assigning Linnaean categories to classifications based on cladograms resulting from phylogenetic analysis (Richter and Sudhaus 2004). Even in earlier phylogenetic publications, such as Hennig (1969), the conflicts between phylogenetic results and categories were well known, and in that publication, Hennig replaced the Linnaean categories by a system of consecutive numbers that directly reflects sister group relationships. However, his system received little attention from the beginning, because in less inclusive taxa, single numbers could be confusingly long (such as 2.2.2.2..4.6..1.1. Trichoptera, the sister group of 2.2.2.2..4.6..1.2. Lepidoptera). Hennig's system seems to have disappeared from consideration.

Since that time, various nomenclatural systems have been proposed to eliminate or replace the Linnaean categories, one of the most recent and popular alternative concepts being the *PhyloCode*. It is beyond the scope of this chapter to present the characteristics, the advantages, and the failures of the PhyloCode, but a critical assessment of the capacity and the limits of Linnaean system will be presented instead. It is still the most popular and widely accepted system of taxonomic ranking, and this is not due to the uncritical persistence of antiquated principles but, conversely, for good reasons. The reader should consult one of the numerous papers on the Linnaean categories and their alternatives for more information, such as Cantino and de Queiroz (2010) in the World Wide Web, Pleijel and Rouse (2003) in favor of the PhyloCode, and the rebuttals of arguments for the PhyloCode and its underlying theories by Nixon and Carpenter (2000, 2003), Carpenter (2003), Schuh (2003), and literature cited therein.

Ranking is an inherent property of any hierarchy in biological systematics, whether it is portrayed in a cladogram or by a formal Linnaean ranking scheme. Since ranking is included in any hierarchy, several unambiguous statements can be made concerning the structure of this hierarchy: for example, if taxon A is more inclusive than taxon B and actually includes B, then B does not contain A. However, the taxon names A and B themselves do not carry any reference per se about their relative position in the hierarchy, that is, whether A includes B, or vice versa, or whether A and B are of equal rank. In complex hierarchies, such as the hierarchy of organisms, the user is concerned with an overwhelming number of taxon names of different relative ranks, and he would be lost if any taxon bore an arbitrary name. Instead, communication is considerably more efficient if the ranking information is stated in addition to the taxon name. The Linnaean categories were invented exactly to convey this information by the use of standardized suffixes (for family group names) and binominal nomenclature for species. As an example, the Cercopithecidae, the Old World monkeys, is usually ranked as a family (indicated by the suffix -idae) and, among others, contains the subfamily Colobinae (with the suffix -inae) (Groves 2001).

The Linnaean ranking system was, and still is, extremely successful, and this is partly because it is easy to understand and to learn. Alternative concepts that have been proposed to replace the Linnaean categories are explicitly rankless. Taxon names still exist, but they do not communicate any information at all about their position in the hierarchy. The user can only understand the hierarchical structure by referring to the underlying cladogram. Hence, discarding Linnaean ranks and the binominal nomenclature results unnecessarily in the complete loss of important information on the taxa. This is not to say that the application of the Linnaean system is always unambiguous. Instead, there are numerous problems involved in taxonomic practice, particularly when portraying complex cladograms in a hierarchical classification. However, it seems unlikely that "[any] single system of nomenclature can ever possess all desirable attributes" (Schuh 2003, p. 60).

Taxa and Categories Are Not the Same

There is a fundamental difference between a taxon and a category. As defined earlier, taxa are groups of real organisms that can be described and named. They can be monophyletic, nonmonophyletic, or phylogenetically untested. In contrast, categories are terms that can be assigned to taxa to connote a certain rank relative to other, more inclusive or less inclusive taxa. Taxa are the objects of biological systematics, whereas categories are a voluntary, notional tool that improves communication among systematists.

Categories and Age

Linnaean categories contain explicit and helpful information about the relative position of a taxon within a certain lineage. The central question in taxonomic practice is, if there is a hierarchy of names that is supposed to reflect a hypothesis of relatedness (or at least overall similarity), how can this hypothesis be aligned with the Linnaean categories in an objective way? To be honest, the "alignment" of the hierarchy of taxa and the hierarchy of categories is determined by practical considerations, which is in the end a matter of subjectivity. However, there is a long-lasting discussion of how to "objectify" the assignment of categories to a specific level in a classification. Actually, all efforts to do this have failed, and future efforts will probably fail. The reasons are easy to understand. Categories, as indicators of relative rank *within* a phylogenetic lineage of organisms, are inherently subjective, at least in a sense. It is a matter of usefulness for verbal communication and of convention and consistency, if, for example, taxon X is ranked as an order or a class. However, neither the hypothetically real hierarchy of organisms nor the categories themselves provide objective criteria on how to applicate them.

However, several approaches to objectify categories have been published. Since phylogenetic reconstruction achieves to reconstruct historical events in the evolution of organisms, it is tempting to try to objectify the assignment of categories to taxa by using age as a criterion. This was already proposed by Hennig (1950, 1966), who discussed the problem of *absolute ranking* of higher taxa in exhaustive details. He suggested that the fossil record allows us to unambiguously define categories by the age of taxa to be classified. His example is the higher-level relationships of insects. Insects are generally considered to be ranked as a class, and since the oldest fossil insects, which belong in the Collembola, have been recorded from the Middle Devonian, the Collembola and their immediate relatives, which must have also been present at that time, would be assigned to what Hennig called a "class stage." This resulted in the following ranking for Collembola: class Insecta, subclass Entognatha, infraclass Ellipura, and microclass Collembola. Hennig, of course, realized that this approach is impracticable and arbitrary. He suggested to "reserve the well-known category designations ("class" and "subclass") for the most important and morphologically isolated groups" (Hennig 1966, p. 185), which can hardly serve an objective criterion. Hennig and subsequent workers were well aware that the age criterion of the categories across organisms or at least animals cannot work, simply because the major evolutionary radiations and subsequent diversifications took place in extremely different periods of time. As an example, the major lineages of the placental mammals that are generally ranked as orders arose in the Cretaceous (Murphy et al. 2001) and thus are comparable in age to the major lineages of Hymenoptera (bees, wasps, and ants), which are considered to be of family rank (Rasnitsyn 2002). If categories could be defined horizontally, the categorical hierarchies of Placentalia and Hymenoptera would have to be adjusted to each other, either by "downgrading" Placentalia to family rank or by upgrading Hymenoptera to class rank. This example clearly shows that a horizontal, *absolute* definition of the Linnaean categories is not only impractical but actually absurd.

However, a *vertical*, relative application of Linnaean categories along a phyletic lineage is a different matter and may be possible as a kind of evidence-based convention. An example is Goodman et al.'s (1998) cladistic analysis of the Primates based on DNA evidence and on extant and fossil morphological characters. Many traditionally recognized taxa appeared to be monophyletic, and their names and ranks as used in current literature were maintained. The ages of these clades were determined using dating evidence as provided by fossils and the model of local molecular clocks. Based on this time scale, clades of roughly equivalent age were assigned the same Linnaean rank. Goodman et al. (1998) analysis resulted in the following dating scheme (category/age [Mio years]/geological period): semiorders/63/early Paleocene, suborders/58–50/late Paleocene to early Eocene, infraorders/45–40/middle Eocene, superfamilies/39–29/middle Eocene to middle Oligocene, families/28–25/middle to late Oligocene, subfamilies/23–22/early Miocene, tribes/20–14/early to middle Eocene, subtribes/14–10/middle to late Miocene, genera/11–7/late Miocene, and subgenera/6–4/late Miocene to early Pliocene.

It needs to be emphasized that an age-related Linnaean ranking might have merits only if applied to clades like the Primates with particular prerequisites. Primates have a widely accepted classificational framework (though the details are still disputed), quite a good fossil record, and cladistic analyses have been published with reliable taxon sampling. If the last common ancestor of the Primates is supposed to be as old as about 63 Mio years, and if the scientific community *agrees* to rank the Primate clade as an order, the highest level of the classification within Primates is defined: clades that arose in the early Paleocene are ranked as orders. Other, younger, fossils can be correlated with a particular rank accordingly. The fossil record, which might include gaps without fossil evidence, is supplemented by the model of the molecular clock, as proposed for Primates. This procedure allows applying the age criterion to any ranking level between the oldest reference point (the putative age of the last common ancestor of the Primates) and the youngest reference points (e.g., the latest splittings to clades generally ranked as subgenera, the youngest fossils).

Approaches like this pretend to be objective in correlating taxa and ranks, at least within the clade they were proposed for. However, it is easy to see that none of the criteria that define the age-rank correlation as proposed by Goodman et al. (1998) leads to an objectively settled ranking. It is a matter of convention if the clade named Primates, which is defined by a set of apomorphies and whose age of origin is defined by a particular fossil, is ranked as an order. Likewise, it is a matter of convention which of the clades within Primates, such as Cercopithecoidea, is assigned superfamily or any other rank. The same arbitrariness applies to the correlation of a clade and an age per se: with respect to the current state of the art in Primate classification, it might be useful to treat the putatively 18-Mio-year-old Cercopithecoidea as a superfamily, but other rank-age combinations might be similarly appropriate if suggested by the total hierarchy within Primates.

Nomenclatural stability is another important issue to be addressed to any classification concept. Stability of nomenclature should minimize changes in the names as they are adopted to changing scientific concepts. Age-defined ranks are, at any hierarchical level, extremely sensitive to the accuracy of the underlying dating of the latest common ancestors. New dating evidence, such as newly discovered fossils or new analytical methods in paleontology or molecular biology, may suggest fundamentally different dates of the origin of particular groups. If, for example, the origin of Primates dates back to 80 Mio years as suggested by Tavaré et al. (2002), the age-related ranking scheme of Goodman et al. (1998) would have to be adopted to the new dating by stretching the ranking range to fit to the longer period of time or by adding more category levels.

The standard approach to calibrating a classification for an age-related application of ranks is to use the earliest known fossils of a particular taxon and to equate their age with the time of origin of this taxon. The resulting age of the taxon under discussion is, obviously, hypothetical and only gives us the so-called *terminus post quem non*, that is, the point of time *after* which the clade cannot have originated. In other words, the fossil record only settles the *minimum* age of the group. This can potentially lead to a serious underestimate of the true time of origin of a clade and, hence, of all other dating results inferred secondarily. As has been pointed out by Martin (2002), this underestimation increases if the fossil record is very patchy. Since this might be the case in many organisms (Tavaré et al. 2002), the oldest fossil of a given clade might be considerably younger than its true stem species. As a result, age-defined ranking schemes are considerably different depending on whether the dating as inferred directly from the fossil evidence, or the dating as indirectly estimated by molecular clock models or estimations of extinction rates and the reliability of the fossil record, is considered.

These applications and problems show that an age-defined, objective correlation of Linnaean categories and clades is as unrealistic, if not impossible, as any other effort toward an absolute definition of ranks. In some cases, such as Primates, age-defined ranks may be useful to some extent, although it must be emphasized that the correlation of ranks and clades even in such cases is at most *intersubjective*, being based on a set of conventions of the respective scientific community. Changing conventions, changing dating evidence, and other factors may considerably alter the putatively objective ranking of Primates. The Linnaean categories are a notional representation of the hierarchical structure of monophyletic taxa representing an inferred, hypothetical sequence of speciation events (or, if a cladistic analysis is still lacking, an a priori assumption of relatedness inferred from overall similarity). As a consequence, the Linnaean system is inherently *relative*, that is, Linnaean ranks denote the hierarchical position of a given taxon relative to other members of the same clade. As has been paraphrased by Schuh (2003, p. 60), "[t]he primary strength of the Linnaean system is its ability to portray hierarchical relationships." It must, however, be emphasized that Linnaean categories are inherently *subjective* in that the exact correlation of a taxon and its rank is not determined by the taxon or the category themselves.

Ranking Fossils

Fossil and recent taxa are basically treated in an identical way in taxonomy. However, if fossils are included in a cladogram, a number of practical terminological problems arise. Fossils are part of the stem lineage of a given taxon, and each single fossil taxon is considered the sister group of the next, less inclusive, taxon. If sister taxa are given the same rank in the hierarchy, each single fossil species that is considered to be the sister species of a taxon that is ranked as an order must be assigned order rank as well. If several fossil species of a given stem lineage in a continuous sequence of sister group relationships with the next less inclusive taxon are known, each of these single species would have to be given a high rank, which would, for example, result in a proliferation of taxa ranked as orders along a single lineage. In principle, each of the pairs comprising a fossil species and its higher sister taxon could also be assigned a new name.

As a consequence, giving a high rank to each of the fossil species would not only appear to be overblown, but this would also ignore the fact that the exact sequence of fossils along a stem lineage cannot be determined accurately in most cases. As an alternative, Patterson and Rosen (1977) have suggested to order fossils according to their hypothetical phylogenetic position but to leave them unranked. Instead, each of these fossils is named *plesion*. The term plesion replaces any rank above the genus level and to tentatively place fossils in cladograms without affecting the hierarchical structure of names and their ranks.

Linnaean Categories as a Communication Tool

Systematists should be aware that the Linnaean categories are a tool for communication. As Griffiths (1976, p. 168) stated, there is no logical reason why taxa *must* be ordered into categories. Linnaean categories do not inherently imply information about the age of a taxon (except if employed within a certain clade by convention, as, e.g., in Primates), the size of a taxon (in terms of species numbers), genetic distinctiveness, or phylogenetic relatedness. The application of a particular rank to a particular taxon is subjective but must fit in the overall hierarchy of the more inclusive taxa.

But Linnaean categories directly mirror the complex, hierarchical relationships in a given clade. Along this lineage, the nestedly ordered categories notionally reflect the nested order of organisms and explicate the relative position of a given taxon to other taxa of the same lineage. The demand for an abolition of the Linnaean categories without substitution involves well-known practical problems and would result in the loss of practical and useful information. There are myriad practical problems involved in the implementation of the Linnaean categories, but this is also the case in any other notional system of ranking. "No single system of nomenclature can ever possess all desirable attributes: i.e., convey information on hierarchical relationships, provide ... stability in the names ..., and provide simplicity and continuity in communicating the identities of the taxa and their relationships" (Schuh 2003, p. 60). Since the discussion about the Linnaean categories reflects the problems how best to express scientific contents linguistically, *applicability* is the central criterion to assess the capability of any ranking concept. The search for the "best" biological nomenclature corresponds to the search for compromise between theoretical demands and practical necessities.

The International Code of Zoological Nomenclature

Systematists and, secondly, subsequent users of the results of biological systematics deal with myriad objects: each taxon, if considered a species or ranked as a genus, family, or order, can be recognized as a biological entity, which, to a varying degree, is distinctly different from other such objects. To enable communication about these objects, in principle, requires the application of unique names, which unequivocally refer to the taxa. Even in pre-Linnaean times, the need to point to groups of organisms by names was obvious. However, before Linnaeus, the names given to taxa were thought to be descriptive or diagnostic terms or phrases rather than proper names, as taxon names are seen today. Although easily recognizable organisms might have been given single names (*uninomina*), or if two closely related forms were known, two-word (*binominal*) names were coined. Increasing knowledge of the diversity of forms made complex, descriptive labels necessary to meet the criterion of uniqueness (e.g., the gentian species that is today known as *Gentiana ciliata* was named *Gentiana angustifolia autumnalis, minor floribus ad latera pilosis* by Bauhin (1623) (Mägdefrau 1992); note that Bauhin and other pre-Linnaean authors already employed unique genus names as more inclusive taxa). Linnaeus, however, introduced a strictly formal nomenclatural system, based on a unique binominal species name. The increasing exploration of remote geographic regions made scientists realize that they are concerned with a seemingly infinite organismic diversity. Due to new discoveries and new techniques, taxon names proliferated. However, it was not only the increase in species descriptions that lead to a rapid increase in the total number of taxon names. Inconsistent or even contradictory terminological systems, development of their own rules by many scientists, replacement of already published names that were considered to be inappropriate or incorrectly formed, and other factors resulted in the strong need for general rules of nomenclature.

Beginning with Linnaeus' works in the eighteenth century, an elaborate body of conventional regulations was developed to provide such general rules. The valid rules of nomenclature in zoology are contained in a judicial text called the International Code of Zoological Nomenclature, here abbreviated as the Code, whose current edition is the fourth. The Code provides a complex set of rules and aims to cover as much of the complexity of the recent and historical naming process as possible. However, cases might show up in which the strict application of the Code might actually threaten nomenclatural stability, and in such cases, every scientist is free to apply to the *International Commission of Zoological Nomenclature* to set aside priority or other provisions of the Code to increase stability. Many provisions of the Code are the result of compromise between conflicting principles, which partly date back to the very beginning of biological nomenclature. Hence, the rules fixed by the Code are far from written in stone but are under constant development. As has been emphatically pinpointed by Mayr and Ashlock (1991, p. 386), "all good law is living law."

An exhaustive description of the Code is far beyond the scope of this chapter, but a few basic principles will be considered here.

Freedom of Taxonomic Thought

The Code does not tell anybody how to classify something or how to recognize species or other taxa. These are scientific decisions that are totally under the responsibility of the systematist. The Code provides rules for a system of communication, a "language," for communicating such taxonomic decisions. This "freedom of scientific thought" is expressly guaranteed in the Preamble of the Code and, indirectly, emphasizes the role of nomenclature in biology as a notional process acting subsequent to the scientific process. As an example, the Code permits a scientist to continue using a name that is considered to be a junior synonym by another author. Conversely, the freedom of taxonomic thought includes also the freedom to make taxonomic mistakes that, as a consequence, do not affect nomenclature. If, for example, a name is erroneously placed in synonymy, its validity is not affected.

New Names and Old Names

The process of naming a newly discovered species properly, that is, in accord with the Code, is surprisingly simple. The Code explicitly provides a set of provisions to be met when describing a species, some of which appear to be commonsense principles. To be usable or, to use the proper term, to be *available*, a name must, first, be *published*. The Codes clearly indicate that distribution "in numerous identical copies ... for permanent record" constitutes a publication. The use of the 26 letters of the *Latin alphabet* for the taxon name is mandatory, although the descriptive text may also be written using a different alphabet. A name must, of course, in principle be *unique* but on different levels: a species name must only be unique in its own genus (there are several animal species with popular species names like *viridis*, meaning green, but no two species (or subspecies) in a genus may bear this name), whereas a genus name must be unique among all animals. However, it is wise to avoid species names that are already in use in closely related genera. In the future, genera might be combined due to changing evidence, which would result in homonymy of such species names. A new species name "must be explicitly indicated as intentionally *new*," that is, by adding a Latin term like "new species" to the newly proposed name or an equivalent phrase or abbreviation. The Code also requires the consistent application of *binominal nomenclature*, which does not apply to names of taxa at ranks above the family group. A new species description must also include an explicit fixation of the name-bearing *type specimen(s)*. A type is an individual specimen to which a given name is attached. In cases in which a taxon previously considered a single species is later split into two species, the species to which the type specimen belongs retains the previously given name. This *type method* is important in taxonomy and will be presented in more detail later. Finally, the Code provides a set of mandatory regulations of more linguistic nature, how new names are to be formed. The most important provision is that names must be either *Latin* or latinized or they must be so constructed that they can be treated as Latin words. Further rules concern practical details such as how names are formed from personal names and other aspects of the correct spelling.

Every scientist who plans to propose a new name for a taxon should consider these simple provisions to be sure that the new name complies with the Code. However, the greater part of the Code is devoted to less simple cases, and most of the problems are caused by names proposed in the past. A smaller part of difficulties systematists face when dealing with previously published names might be caused by the erroneous application of the Code or by erroneous taxonomic decisions. The majority of problems, however, simply portray the continuously changing concepts and applications in the 250-year-old history of biological systematics. Such changes might affect scientific content (e.g., by the invention of alternative species concepts) or might be more formal (e.g., the explicit designation of a name-bearing type was not mandatory at the beginning of biological systematics). As a result, historical names are not only hard to locate in the literature in many cases, they often require time-consuming, elaborate efforts to clarify the correct original spelling, the presence of type material, the identity of the species, the correct date of publication of the original description, and several other potential difficulties. Two of the most common problems that come up when dealing with historical names are *synonymy* and *homonymy*.

The fact that a considerable portion of taxonomic practice is unusually time-consuming when compared to the outcome, i.e., the clarification of a single species name, is part of the legacy of about 250 years of biological systematics. In many groups of organisms, taxonomists are condemned to spend most of their time interpreting the work of pre-twentieth-century systematists. “The past [often] acts as a dead weight on the subject, the complex synonymy and scattered type material deterring anyone from attempting a modern revision” (Godfray 2002, p. 17).

Validity, Synonymy, and Homonymy

As has been explained earlier, a taxon name must fulfill a set of conditions to be available in terms of Code compliance. Among the available names, only the oldest available name is what systematists call *valid* and has *priority* over the younger names. The valid name of a taxon is sometimes referred to as the *correct* name, which means that open nomenclatural problems have been solved and that a single name retained, which under the provisions of the Code is the only approved one. The date of publication of the original description of a name is thus of crucial importance and must be carefully determined. It must be emphasized that the principle of priority applies to the species, genus, and family levels only but not to levels above the family rank.

In by far the most cases, the valid name is the oldest name. Exceptions occur when the oldest name, in case of a species, is already in use in the genus, resulting in homonymy. Then, the younger of the homonymous names would no longer be valid but must be replaced by the next available name of the same species, if any exists. An example is a subspecies of the common chimpanzee, *Pan troglodytes verus* Schwarz, 1934 (originally described as a subspecies of *Pan satyrus* Linnaeus, 1758, the species name of which was suppressed by the International Commission on Zoological Nomenclature in 1999). The oldest available name of this subspecies is *Simia chimpanse* Matschie, 1904, but despite having priority due to the early publication date, Matschie’s name cannot be used because it is a junior homonym of another species, *Satyrus chimpanse* Mayer, 1856. Since *Satyrus chimpanse* Mayer is considered to be identical to, that is, a synonym of, the nominate subspecies, *Pan troglodytes troglodytes*, the species group name *chimpanse* occurs twice within *Pan*, by Matschie, 1904, and by Mayer, 1856, respectively. This is called *secondary homonymy*, since the two names under discussion were first proposed in different genera and got in conflict after being considered to belong in the same genus. *Simia chimpanse* Matschie was published half a century later than *Satyrus chimpanse* Mayer, and thus the younger of the two names must be replaced. The next available name is *Pan satyrus verus* Schwarz, published in 1934, which then becomes valid. In many species, however, no name is available other than the originally proposed name. Then, the revising author has the authority to propose a replacement name, which then becomes available with the reviser as the correct author and the date of his publication.

If a single taxon is given two or more names, each of these names is a *synonym*. The earliest published synonym is referred to as the *senior synonym*, even if it is considered to be the valid name. Any other earlier names of the same taxon are called *junior synonyms*. In most cases in practical taxonomy, systematists are confronted with the question if two independently published species names that were based on different name-bearing types actually represent the same species. This kind of synonymy with different types is called *subjective synonymy* because it expresses the scientific conviction of the revising author that the two names refer to the same thing. Names applied to a species on the basis of the same type specimens are *objective synonyms*.

Typification: Establishing Objective Reference Points

The type method is a guiding principle in biological systematics. In taxonomic practice, the identity of species, particularly when described in the past, is often difficult to establish due to insufficient descriptions or illustrations. As a result, historical species descriptions might apply to more than one currently recognized species. Due to new evidence, taxa might be split up into two or more less inclusive taxa. In all such cases, it might be difficult to establish which of the newly separated taxa has to retain the original name and which should be newly named. This problem is solved by the invention of objective reference points, the types. Types in the broadest sense are zoological objects to which a name is firmly tied. The type of a species is always a single specimen, the type of a taxon at genus rank is a species, and finally, the type of a family-rank taxon is a genus. If a previously described species is considered to be actually composed of more than one species, the type specimen fixes the original name to the species, to which it belongs. The same holds for taxa at the genus and family ranks.

The Code permits the use of a few different kinds of types in taxonomic descriptions. At the genus and the family level, only type species and type genera exist, respectively. A *holotype* is always a single specimen, which is either the only specimen available for the original description or it is explicitly selected out of the original series of more than one specimen to give it precedence over the other specimens, which then are called *paratypes*. In current species descriptions, the explicit designation of a holotype is mandatory. Paratypes do not have special standing under the Code but should be explicitly mentioned as members of the original type series by calling them paratypes. If the original describer in older publications mentions more than one specimen but did not select a holotype, all type specimens are the *syntypes*. A syntype series is of little help in conflicting taxonomic situations because they might actually belong to more than one species. In such cases, a revising author has the authority to subsequently select a single specimen from the original type series, which then would be called a *lectotype*. Accordingly, the remaining syntypes would be the *paralectotypes*, which, again, are only of secondary importance. If the type material of a species is considered to be lost, the revising author may select a specimen that was not part of the original type series, as a *neotype*. In some cases, the lack of type material is of minor importance because the identity of the species is obvious. An example is *Homo sapiens* Linnaeus, 1758, for which no type specimen or specimens have ever been settled (Spamer 1999). A neotype must be designated only if this action facilitates nomenclatural stability so that the name is properly and consistently applied. Since a neotype is required in cases with unsettled and problematic nomenclature, one can almost never be completely sure if the neotype and the original types are really conspecific. Thus, designation of a neotype might be risky and should only be done if absolutely necessary. Numerous other kinds of types have been used in the literature, but only those above are still permitted under the current Code. Examples of types that are not regulated by the Code are allotypes (a specimen of the opposite sex of the holotype, actually simply a paratype) or topotype (a specimen originating from the type locality of the species to which it is thought to belong).

Incidentally, it is a wide held belief that the type specimen or specimens of a newly described species must be dead or should be killed sooner or later to be finally deposited in a museum collection or in another kind of persisting and accessible environment. This means that in most cases, a new species description is based on one or more specimens that are physically available to the scientist during the process of writing the description. The Code requires that the specimen (the holotype) or specimens (syntypes) on which the name is based must be explicitly stated and accompanied by description or diagnosis to differentiate the new taxon. However, this requirement does not include any mandatory provisions about the physical availability, detailed morphological description, or depository of the type specimen (Wakeham-Dawson et al. 2002).

A type specimen need not be especially *typical* for the species to which it belongs. Its function is simply that of a “name bearer” (Simpson 1961). There are several potential criteria for how to select a holotype out of the entire material that is available to a scientist. If the species is differentiated from its congeners by means of complex morphological features of the male genitalia (as is common in invertebrates), it might be appropriate to make a male the holotype. Sometimes, not all type specimens are complete or show the diagnostic characters equally well. It would make sense to choose as the holotype a specimen, which exhibits most or all of the characters that are of diagnostic value at the time of description and with respect to new future discoveries as far as can be predicted.

The description of a new species is always based on all specimens available at the time of description. Since the holotype is just a name bearer, its function is not to serve as the only basis of the original description (except when only a single type specimen is known).

Fossils, Fragments, and Heterogeneous Type Specimens

The Code applies to both living and extinct animals, as is explicitly stated in its Article 1. Thus, the principles of the type method as briefly presented earlier with reference to recent species are equally applicable in paleontology. However, many fossils, particularly complex multistructured organisms, such as vertebrates, inherently lead to practical problems. In most fossil vertebrates, only hard structures are fossilized and thus preserved. In the course of diagenetic processes, soft tissues that connected the hard elements in the living animal are usually decayed so that the resulting skeleton falls apart. In the ideal case, the preserved elements remain in their original position after embedding in a fossilization matrix so that the elements can be easily associated with each other. In many cases, subsequent physical processes might have altered the relative position of the elements or have destroyed parts of the organism.

Fossil hominids are never completely preserved, not even with respect to bones. Sometimes, just a single preserved bone is sufficient to provide evidence for taxonomic identity. If a single bone is the basis of a new taxon, just the bone is referred to as the holotype. An example is the holotype of *Homo heidelbergensis* Schoetensack, 1908, which consists of a complete, adult mandible. There is no ambiguity about the formal basis on which the new species is based. If more than a single element is available, association to individual can be difficult if the elements are not in the original position relative to each other but are more or less dislocated or destroyed. An example is the composition of the types of *Homo habilis* Leakey, Tobias, and Napier, 1964. Several fragments assignable to the new species were available such as mandibles, isolated teeth, parietal and hand bones, and cranial fragments. Due to external evidence, such as the position of the fragments as found during excavation, the fragments could be associated with five individuals. The holotype of *H. habilis* consists of a mandible with dentition and the associated upper molar and parietal and hand bones, originating from a single juvenile individual.

These examples show another principle of the type method. A type is always a zoological object but is not necessarily something that is or is close to a complete organism. A single tooth, an isolated wing, or any other part of an organism is in principle sufficient to serve as the basis for a new species. In a way, incompleteness is an inherent attribute of most preserved specimens because many preservation techniques result in the loss of some characters. Pinned, that is, dried insects and stuffed, mounted vertebrates have usually lost all or most of their soft tissue. Thus, even if a specimen has lost almost the entire physical structure except for a single tooth, this incompleteness of a specimen does not prevent potential type status. It is, however, wise to associate isolated fragments such as a molar and a mandible to a single type specimen only if the evidence is unambiguous. If subsequent evidence is found that the fragments actually belong to different individuals, this might cause a lot of unnecessary nomenclatural confusion.

Conclusion

Names can be seen as the key to biodiversity. Names serve as unique identifiers or tags, which unequivocally refer to biological species and higher taxa. Names form the essential language to communicate about biodiversity. The naming process in biology is an intellectual challenge which happens subsequently to the process of scientific discovery and description. New methods and tools for the discovery of the largely unexplored species diversity on earth have been established in the past decades, which have increased the rate of species description in an unexpected amount. In order to fulfill its function as a tool for an effective organization of biological data, a set of rules needs to be followed to make scientific names unique and unequivocal. Modern taxonomy, the science of naming, identification, and classification of organisms, is an integrative approach, which combines a wide range of methods, tools, and theories for both the recent and past diversity.

Cross-References

- ▶ Fossil Record of Miocene Hominoids
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Neanderthals and Their Contemporaries
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Species and Diversity of Australopiths
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Species Concepts and Speciation: Facts and Fantasies

Colin Groves

Contents

Abstract

The identification of the punctuated mode of evolution, an alternative to gradualism, has required renewed focus on the nature of species. A species is an evolutionary lineage and may be recognized by having fixed (absolute) heritable differences from other species. Among the various modes of speciation which have been proposed, allopatric speciation is the best authenticated; it can be

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C. Groves (✉)
School of Archaeology & Anthropology, Australian National University, Canberra, ACT, Australia
e-mail: colin.groves@anu.edu.au

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divided into dichopatric and peripatric. Other modes are parapatric, sympatric, stasipatric, and, one which has recently assumed a considerable importance, speciation by hybridization. All these must be considered when thinking about how the various species identified in the hominin fossil record originated.

Introduction

Whereas taxonomy is a product of the human mind, species have a real existence (see, e.g., *Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms*, in this Handbook): a species is an individuated evolutionary lineage and has been compared to an individual organism. All too many people use the word "species" without really understanding this important distinction, and a consequence of this misunderstanding is the prevalence of catchphrases like "taxonomic inflation" and "how much difference do you need for a species?" Once it has been clearly understood that a species is a lineage, then we can ask meaningful questions of evolutionary theory, such as – How do new species originate? How long does speciation take? Is sympatric speciation possible? How frequent are hybridization and gene flow between species? What is the role of reticulation in the formation of new species? And we can ask informed questions of the fossil record, including – How many hominin species coexisted at any one time? How do we recognize species in the fossil record? And we can inquire about the very origin of hominin species.

The PE Revolution

It is probably true to say that until 1972, most paleontologists had interpreted their fossils as showing gradual change with time, and if they did not show gradual change it could be inferred as failure to demonstrate much, or any change could be put down to the incompleteness of the fossil record. The year 1972 saw the appearance of the paper by Eldredge and Gould introducing the concept of punctuated equilibria (herein after PE), in which they proposed that the major process of evolution is not, after all, one of gradual modification, but a series of stops and starts: there are long periods when nothing happens, succeeded by short bursts of rapid change. The bursts of change, moreover, are not in the central, paleontologically most visible, population of the species, but in small peripheral populations which then have the capacity to invade the center and usurp the parent population.

Long ago, Simpson (1944) had recognized that evolutionary change occurs at different rates; along his rate spectrum he distinguished horotely ("normal" or average rates of evolution), bradytely (unusually slow), and tachytely (unusually fast). Early critics of PE assumed that PE was merely a resurrection of these old Simpsonian categories. But it is not mainly about this: it is about stasis and speciation. Simpson was of course well aware of stasis: he described how in many cases a fossil species did not change at all over a considerable segment of time but remained the same. He, too, was aware of the importance of speciation. From the process of evolution along a single lineage (anagenesis), which he did seem to consider primary, Simpson (1944) carefully distinguished cladogenesis (evolution by splitting of one lineage into two); this typically results in two species resulting where formerly there was one, so cladogenesis can be thought of as, broadly speaking, equivalent to speciation. What Eldredge and Gould had observed was that in many cases long-term stasis is followed by the sudden appearance of a different species which replaced the earlier one. The real innovation of PE was to insist that it is stasis, not anagenesis, that is the usual state of affairs and that speciation, not anagenesis, is the engine of evolution.

Eldridge and Gould were perfectly aware, of course, that they had intellectual precursors. Three of these were especially influential. One of these was Richard Goldschmidt, a geneticist who in 1940 proposed the "hopeful monster" hypothesis, under which major evolutionary changes occurred abruptly. The "hopeful monster" was not part of the original package, but it was espoused in later versions by Gould (1990, 2002). A mechanism for "hopeful monsters" was later proposed by Schwartz (1999).

Another inspiration for PE was Mayr who, in 1963, urged the founder principle as a mechanism of speciation. In founder principle theory, a small segment of a species becomes isolated from the rest (e.g., by geographic or environmental change) and undergoes rapid genetic differentiation. He preferred this mechanism (now often called peripatric) to the generally assumed view that a species, when it becomes divided, splits into two fairly equal halves which then diverge gradually (dichopatric). Schopf (1972), in his editorial introduction to the paper, traced the idea of founder principle back to Haldane in the 1930s and even as far back as Bernard in the 1890s, but there is no doubt that it was Mayr whose careful and detailed formulation of the principle established it as a significant mechanism – or even *the* significant mechanism – of speciation.

The third major influence on the genesis of PE was another geneticist, Sewall Wright, who in a series of papers (see especially Wright 1968) formulated the principles of genetic drift, which is the random change in gene frequencies. As he showed mathematically, later elaborated in detail by Kimura (1983), stochastic processes have a small but finite probability of resulting in the fixation of new genetic variants, even in the face of weak negative selection.

Where does this leave anagenesis? Long-term trends in evolution of course exist. It is how to explain them which has been the problem. Osborn, in 1936, ascribed evolutionary trends to orthogenesis, a sort of (internally controlled) urge to progress onward and upward, always in the same direction. Simpson (1951) effectively demolished orthogenesis and instead proposed what he called orthoselection, in which natural selection forces fairly consistent change in one direction as long as local environments favor it. Eldredge and Gould (1972) suggested how PE might explain evolutionary trends, but the problem was more fully considered by Vrba (1980) whose "effect hypothesis" has become part of the theoretical core of PE. We will return to the matter of long-term trends in a later section.

So we have two apparently opposed models of the evolutionary process. Gradualism allows for anagenesis to be a major evolutionary mode, though it does not mandate it; if, for example, lineage splitting does occur, it is under the gradualistic model followed by the slow mutual divergence of the two daughter lineages. Under PE, it is cladogenesis which is definitely the major evolutionary mode; when lineage splitting occurs, it is asymmetrical, and by the founder effect one daughter lineage diverges but the other generally does not. The major problem that lies at the heart of the difference is the nature of speciation.

The Nature of Species

Species: Theoretical Concepts

Before we can even consider what speciation involves, we must very carefully delineate the nature of species. If we are to contemplate whether species, which are already regarded as the units of ecology, biogeography, and nowadays of conservation strategy, are also the units of evolution itself, then we must be clear exactly what species are. The importance of what we mean by the word "species" goes way beyond systematics, the field of study for which the term was invented.

It is unfortunate in one way, appropriate in another, that there is quite a multitude of different conceptions of what a species actually is. How many "species concepts" one distinguishes is a matter of how finely one is prepared to seek out the fine distinctions between different authors' manner of phrasing. Thus, Harrison (1998) distinguishes only seven and Mayden (1997), and following him Hey (2001), as many as 24. Broadly, we may divide them into those which emphasize the absence of interbreeding and those which do not: "theoretical" and "operational" concepts, in the terminology of Groves (2001). The division also corresponds, in broad terms, to "pattern" versus "process": the pattern that we can observe versus the process which maintains it or brought it about in the first place.

For Dobzhansky (1937) and Mayr (1963), the nature of species lies in its reproductive isolation from other species. This view of reproductive isolation as the defining feature of species is called the biological species concept (BSC). Species were defined by Mayr (1940) as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups," while Dobzhansky (1950) summarized the situation by saying that the species is "the largest and most inclusive… reproductive community of sexual cross-fertilizing individuals which share in a common gene pool."

Reproductive isolation in turn depends on reproductive isolating mechanisms, which may be either premating or postmating. Premating mechanisms are what prevents potential mates from meeting (seasonal or ecological), or from mating if they do meet (ethological), or from permitting sperm transfer if they actually get as far as mating (mechanical). Postmating mechanisms are what prevents gametes or zygotes from surviving if mating has nonetheless successfully occurred, or hybrids from surviving, or hybrids from breeding if they do survive.

Paterson (1978, 1980, 1982) argued that postmating isolation cannot be more than a symbol of species status: two sexually reproducing genotypes, A and B, do not avoid interbreeding with each other as such, instead A selects other A individuals and B selects other B. They do this by means of specific mate recognition systems (SMRSs): one individual emits a signal to which another responds. A species, for Paterson (1978, 1982), is a population (or group of populations) whose members share a common SMRS: he calls this the recognition species concept. Examples of SMRSs could be vocalizations, such as the distinguished species of bush babies or galagos (Primates: Galagidae), whether sympatric species pairs (Masters 1991; Nash et al. 1989) or allopatric populations within what had previously been deemed unitary species (Bearder et al. 1995); or facial markings, together with the facial expressions, head flagging, and whole-body movements that serve to emphasize these markings, as between species of the genus *Cercopithecus* (Kingdon 1980, 1988). In principle, all one would have to do would be to look at facial patterns in two given populations of animals and, if they are different, separate them as different species. But how much difference is "different"? And what if members of the two populations do, nonetheless, interbreed? The same question could be asked about vocalizations: how "different" do they have to be to qualify?

Templeton's (1989) cohesion species concept is another attempt to modify the BSC. In this concept, a species is defined by the genetic and demographic mechanisms which give it its cohesion: the genetic mechanisms are those which limit its gene flow with other species, and the demographic ones are those which constrain it to its "fundamental niche." This tries to fuse the original BSC with the recognition concept while incorporating a general appreciation that a species must have its own ecological niche; but one would be hard put to use such a concept in practice.

The BSC and the attempts to modify it work very well in cases of sympatry; at least in most cases, although in some populations of a species, the presence of mtDNA characteristic of a different (sympatric) species hints at past gene flow (see below). If two taxa are sympatric, then they are reproductively isolated: they are distinct species, and no further discussion is possible. If they are parapatric, then equally they have the chance to interbreed, and do not. But what if they are allopatric? Several authors have emphasized that the BSC is simply not applicable in cases of allopatry. Berlocher (1998) noted that the first author to point this out was A.R. Wallace himself, in a paper written in 1864.

Mayr et al. (1953; see also Mayr 1969) offered three criteria to decide whether two allopatric taxa are distinct species, or merely subspecies. The amount of difference between allopatric taxa should be compared to that between:

(1) Sympatric taxa in the same group
(2) The most divergent intergrading subspecies
(3) Freely hybridizing populations in the same group

The first criterion founders on such things as the existence of sibling species, i.e., those that are nearly indistinguishable, which nonetheless may vary geographically. Both Dobzhansky and Mayr emphasized the importance of sibling species and described cases in detail, but did not comment on how their very existence renders criterion (1) impossible. As for the second criterion, "degree of difference" is not strongly correlated with the propensity to interbreed: the two most distinctive species of baboons, the hamadryas baboon *Papio hamadryas* and the Olive Baboon *P. anubis*, interbreed along their common geographic border. The third criterion depends on the ability to distinguish between primary and secondary intergradation which, if the hybridization is too “free,” may be a very subjective matter indeed. When all is said and done, “amount of difference” is a very slippery concept, whether we consider morphology, vocalizations, DNA, or any other type of differences.

If we require that a species must be monophyletic (but see below), then we have another problem with the BSC and its modifications. The relationship between common descent and interbreeding has been explored by de Queiroz and Donoghue (1988), who conclude that they may or may not coincide. If they do not, then a species will not be monophyletic.

A different problem is a purely practical one: how do we know, in any given case, whether reproductive isolation really exists or when we are dealing with SMRSs? Detailed field observations may inform us in the end, but these are not available in most cases – whether to test for the reality of SMRSs or for the existence of reproductive isolation.

Yet we have to agree that reproductive isolation, in the cases where it can be demonstrated, is decisive. Many authors, including Groves (1989), have been so impressed by this that they have treated “speciation” as equivalent to “the evolution of reproductive isolation.” And how this occurs is indeed an important question: is reproductive isolation a by-product of divergence, as argued by Harrison (1998), or can it be its cause, as argued, for example, by the advocates of sympatric speciation?

Species: Operational Concepts

If one is working with preserved animals in a museum, or with the fossil record, the species criterion of the BSC – however much one tinkers with it – can be at best an inference, at worst misleading. As Nixon and Wheeler (1990) put it, what can be observed under such conditions can only be patterned, not processed. This was observed more than 30 years ago by Sokal and Crovello (1970) and was the reason why they rejected the BSC, though they did not explicitly propose an alternative; it was left to Cracraft (1983, 1989, 1997; see also Eldredge and Cracraft 1980) to propose the phylogenetic species concept (PSC), under which a species is regarded as the minimal cluster of individuals (i.e., a population or group of populations) that is diagnosably distinct from other such clusters.

The concept was called “phylogenetic” because, under it, species are the terminal points on a cladogram; hence they are the least inclusive phylogenetic units. But it stands to be misunderstood; Avise and Ball (1990), Mallet (1995), and Harrison (1998) all misread it as specifying that a species must be defined by apomorphies. This is not the case: a cladogram depicts sister-group relationships, not ancestors, and a terminal need have no autapomorphic states. It is therefore perfectly possible under the PSC to have a species that is defined only by primitive retentions, a "living fossil" in the broad sense. It follows from this that a species may not be demonstrably monophyletic: indeed, the implication of speciation by founder effect would be that, initially at least, up to half of all species are not. Baum (1992) refers to such nonmonophyletic ancestral forms as metaspecies.

There is also some disagreement over what exactly is distinct under the PSC. "Diagnosably distinct" (Cracraft 1983) may mean one diagnostic character state ("at least one": Baum 1992), or it may require "a unique combination" (Nixon and Wheeler 1990; Christofferson 1995). In the main the case may be academic, but in the extreme case a single fixed heritable difference from its relatives still allows a population to be diagnosable, hence to be a species. But remember that fixed heritable differences may in fact be expressed only in one sex or at one stage in the life cycle. Under the PSC, therefore, species are units of genetic cohesion – not necessarily of reproductive cohesion, contra Kimbel and Martin (1993), because different phylogenetic species may still interbreed.

The PSC is eminently operational. While we can rarely or never be entirely certain that a given character state is fixed (i.e., at 100 %), the PSC relies on the evidence at hand, while the BSC and its modifications demand that we go in for a great deal of inference. Paleontologists have little option but to use the PSC (*contra* Gould 2002:785–789), and in reality neontologists usually have no option either.

What Are the Different Species Concepts Trying to Say?

The Evolutionary Species Concept (ESC) was proposed by Simpson (1961): "A lineage... evolving separately from others and with its own evolutionary role and tendencies." Subsequent authors have modified this, or drawn it out, in different ways; thus, Christofferson (1995) explains that, as far as sexually reproducing organisms are concerned, a species is "a single lineage... genetically integrated by historically contingent events of interbreeding."

The supreme importance of this concept is acknowledged by all commentators; it is the very essence of the species – why the species category is so vital (Mayden 1997) – and is why Ghiselin (1974) reified species as "individuals." It is therefore a different level of concept from either the BSC or the PSC. The fact that Simpson's definition (or Ghiselin's gloss on it, for that matter) cannot be used in decision-making returns us to the PSC as the means whereby we can recognize species.

The evolutionary concept of species was extended by de Queiroz (2007), who argued that this is fundamental: a species is quite simply an evolutionary lineage and that what have in the past been termed "species concepts" are simply different types of evidence for lineage separation; the existence of any one of the properties that have been thought crucial for recognizing species (reproductive isolation, a specific mate recognition system, diagnosability, genetic distance) is evidence for the existence of a species. It follows that, given that the property that delimits species at base is always fixed heritable differences, what we have been calling the PSC, more correctly phylogenetic evidence in de Queiroz' terminology, takes primacy.

When Groves (2001) reclassified the Primates on the basis of the PSC (rather tentatively, probably too tentatively, in some parts), there was little demur: other primate specialists in the main adopted the idea without problem (see, however, Tattersall 2007, and, more recently, Rosenberger 2012). It was when the concept was applied to very large mammals (Groves and Grubb 2011) that strong objections were raised (see especially Zachos et al. 2013), although this reaction, insofar as it was based on reasoning rather than horror at "the shock of the new," was rooted in a series of misunderstandings (Groves 2013; Gippoliti and Groves 2013).

Does Species Status Necessitate a Certain Degree or Quality of Difference?

The literature on species, including in mammals, is full of statements implying that differences between species are of a different order or degree to those between subspecies, populations, or individuals within a species. Often, there are no explicit statements to this effect; rather, it is assumed that this is so, that in some character or other species differ grossly or qualitatively (however that is interpreted), whereas mere subspecies differ quantitatively: thus, between- and within-species differences are not of the same kind.

Bohlken (1958), for example, used an allometric method. He found that on his bivariate plots of skull and horn measurements, different species of Bovini generally have different slopes, and when by contrast he found that two of them (the tamaraw, *Bubalus mindorensis*, and the Indian wild buffalo, *B. arnee*) did not, he used this as a reason for combining them into one species. Imaizumi (1970) also used a variant of this allometric method with respect to Japanese and Chinese deer (*Cervus nippon* group); in this case he plotted skull variables against an index of temperature, on the hypothesis that different species would show different responses to Bergmann's rule whereas different subspecies within a species would respond similarly.

The idea that species ought to be more differentiated genetically than infraspecific groups has a long history. In a classic paper, Ayala (1975) compared values for identity (Nei's I) and distance (Nei's D) at various loci for various animal groups and found that well-differentiated species pairs characteristically have higher values of D than do sibling and sister species which are higher than subspecies which in turn are higher than local populations. Thorpe (1983) collected an even larger amount of data, also using Nei's D, and he too concluded that there is an average difference between species and infraspecific levels. Bradley and Baker (2001) tested genetic distances at different taxonomic levels using cytochrome-b sequence data for a number of bat and rodent genera and once again found that genetic distances do tend to increase in the expected sequence from interpopulational to interspecific; moreover, distances between presumed sister species were less than between congeneric species in general. (The same was found, for a different region of mtDNA, for species of *Macaca* by Hayasaka et al. (1996).)

This of course makes sense under molecular clock assumptions. Avise and Ball (1990) demonstrated by computer simulations that the longer two populations have been separated, the more loci should differentiate them (although smaller effective population sizes will reduce the time it takes for them to become reciprocally monophyletic); if it is true that species have been separated for longer than infraspecific populations, then one should expect that on average there should be higher genetic distances between them.

But scanning Ayala's tabulations, one can observe that the values of D for the four levels overlap widely, at least in his vertebrate examples: well-differentiated species pairs may actually differ *less* than do sibling species, species of any kind frequently differ *less* from each other than do subspecies, and subspecies may differ *less* than do taxonomically undifferentiated local populations. In Thorpe's (1983) dataset, again, the overlap between levels is enormous. One would be foolhardy to insist that above a certain level, two taxa are merely subspecies, while below it they are species.

On average, species of the same species-group differ in their cytochrome-b positions by 9.55 % in rodents but only 6.83 % in bats (Bradley and Baker 2001:963, Table 1) and 7.86 % in macaques (Hayasaka et al. 1996:1048–9, Table 2, and some extra distances calculated from Table 1). But these are average differences; it is possible for different species to differ by much less than this – as little as 2.23 % in the smallest of the rodent comparisons, 2.50 % in bats, and 3.72 % in macaques. The conclusion, and it is a very important one, is that we must simply adjust to the fact that well-differentiated species pairs may show extraordinarily little sequence divergence in a given DNA region. The genetic species concept of Baker and Bradley (2006) is more a recipe for detecting the existence of cryptic species than a species concept itself.

Hybridizing Species

Reproductive isolation may or may not be a result of speciation, and the old controversy over whether such RIMs may exist and precede the evolution of species-specific diagnostic states, or are a by-product of them, is unresolved. But it is evident that species that hybridize are not necessarily each other's closest relatives: cases are known where sister species are intersterile, while less closely related species are not (Baum 1992).

Hybrid zones between distinct species are referred to as tension zones (Key 1968). Their width depends on migration, which acts to widen the zone, and selection, which acts to reduce it (Barton and Hewitt 1985). The most stable hybrid zone is one which follows an ecotone; it widens and narrows in different regions and apparently tracks the ecotone over space and time (Arntzen and Wallis 1991). Whether it persists over long periods of time is arguable; can there be selection against individuals that lack a focused search image, such that they waste their reproductive effort by producing hybrids? Paterson (1978, 1980) argued strongly that such reinforcement is unlikely; Barton and Hewitt (1985), on the contrary, considered that reinforcement may in fact occur, although it is only one in a number of factors which may help to maintain the zone.

There are several well-analyzed cases of hybridization between perfectly distinct species. Two newts, *Triturus cristatus* and *T. marmoratus*, are broadly parapatric in western Europe, where they are characteristic of flat, open country and more hilly, wooded regions, respectively (Arntzen and Wallis 1991). They hybridize in places, and the hybridization appears to be one way, as hybrids all possess *T. cristatus* mtDNA. The authors argued that there was a selection against hybrids because of both theoretical grounds (chromosomal incompatibility) and high frequency of digital anomalies among them; they did find, none the less, evidence that genes had leaked across the hybrid zone into the "pure" species on either side. Whereas for Key (1968) this would have been reason enough to combine the two species into one, Arntzen and Wallis (1991) argued against such an interpretation on the grounds that the two essentially maintain their genetic integrity overall, and even in the hybrid zone itself only 4 % of the population are F1 hybrids.

Among mammals the classic study of a hybrid zone is that by Hunt and Selander (1973) on two commensal mouse species, *Mus musculus* and *Mus domesticus*, across the width of the Jutland peninsula, Denmark. This hybridization process too is asymmetric; mtDNA from one species leaks some distance well beyond the hybrid zone proper into the other species, although interestingly this does not apply along the same species boundary in southern Germany, where the mtDNA and nDNA boundaries are concordant.

Species do not have to form actual hybrid zones: well-differentiated sympatric species may also hybridize. *Cercopithecus ascanius* and *C. mitis* hybridize sporadically in East African forests, and in Gombe Stream National Park, this is so common that the frequency of hybrids is comparable to that of the parent species (Detwiler 2002). But hybridization need not be quite as blatant as this: phenotypes may be for all intents and purposes unaffected, and only the foreign mtDNA remains as a kind of fossil of recent or more remote episodes, as in the case of two species of deer (*Odocoileus*) in Texas which appear quite distinct but may possess the other species' mtDNA (Ballinger et al. 1992).

A phenomenon occurring in many hybrid zones is the high frequency of rare or otherwise unknown alleles, termed hybrizymes (Woodruff 1989). They may result from recombination within loci, increased mutation, or relaxed selection. The very existence of hybrizymes suggests that, for whatever reason, new genetic features may arise in hybrid zones (or perhaps more probably they survive there, where they do not within the pure species) and is clearly part of the general phenomenon of transgressive segregation (Rieseberg et al. 1999), whereby extreme phenotypes are generated by the crossing of poorly compatible genomes.

More recently, it has become clear that there are entire species of hybrid origin in animals, analogous to those which have arisen by polyploidy so frequently among plants. A striking example has been deduced in mammals: the stump-tailed or bear macaque, *Macaca arctoides*, has Y chromosome sequences typical of the *M. sinica* group but mtDNA sequences similar to *M. fascicularis* (Tosi et al. 2000), and most likely the species is derived from an asymmetrical hybridization event. *M. arctoides* is very far from being morphologically intermediate between its presumed parental species and has obviously changed a good deal since it was first generated. Other examples of species that may be of hybrid origin are the wisent or European bison, *Bos bonasus* (Verkaar et al. 2004), and Père David's deer, *Elaphurus davidianus* (Meijaard and Groves 2004).

This phenomenon, known as reticulation (literally the interweaving of different lineages), is an unexpected addition to our understanding of evolution. It in no way challenges the status of the species as an evolutionary lineage: there is no reason at all why genes, including mtDNA (which is of course a single genetic locus), cannot be incorporated from other species as long as a species maintains its own evolutionary identity and remains, in the jargon, "individuated."

Indeed, multiple cases of introgression and evident speciation by hybridization have become known among Primates. They seem to be especially rampant among Colobinae (Wang et al. 2012; Liedigk et al. 2013), but a good case has also been made for introgression into the early hominin gene pool by proto-chimpanzees (Patterson et al. 2006).

Speciation

How Does Speciation Happen?

The literature on speciation is considerable (Barton 2001), but one cannot improve much on the categorization by White (1978) into seven general modes:

(1) Strict allopatry without a population bottleneck. This is dichopatric speciation: ordinary vicariance on either side of a newly arisen barrier, such as a river changing course, when the two daughter populations are both large. If selection is not operating to push the two apart, they still have a low but finite probability of slowly diverging by stochastic processes as modeled by Kimura (1983).

(2) Strict allopatry with a narrow bottleneck of one component. This is of course founder effect; typically, the component that is not bottlenecked remains identical to the parent species, while the bottlenecked component diverges rapidly (peripatric speciation).

(3) Extinction of intermediate populations in a chain of races. There is commonly some clinal variation through the range of a species and, if geographically and morphologically intermediate populations go extinct, the end points will be already somewhat differentiated. It is, consequently, a form of dichopatric speciation. There is some fear that this process may be happening today as populations of widespread species vanish in all but a few isolated reserves, and this pseudo-speciation must be carefully studied to differentiate it from genuine dichopatric speciation (e.g., in the latter case, much deeper divergence can be expected in key DNA sequences).

(4) Clinal speciation. A cline may become stepped over time, resulting in parapatric speciation.

(5) Area-effect speciation. If incompatible alleles or gene complexes arise in different parts of a species' range and spread, there may be selection against hybridization when they meet.

(6) Stasipatric speciation. This was White's own discovery (White 1978, 1979). A chromosomal rearrangement arises and spreads despite low heterozygote fertility and becomes established as soon as its frequency increases to the point where homozygotes begin to be generated. This process, as discussed by Bush et al. (1977) and Meester (1988), creates new linkage groups and breaks up old ones, which might affect gene expression; it may be promoted under some forms of social organization such as clans and harems by limited vagility and dispersal, by distributional patchiness, by individual territoriality, and, generally, by low effective population size.

(7) Sympatric speciation. This is the one guaranteed to start fistfights in bars. Mayr (1963) argued strongly against it, but from time to time it has nonetheless surfaced as a real possibility. Maynard Smith (1966) argued that differential habitat assortment could lead to speciation in the absence of any geographic separation; Bush et al. (1977) urged that it might even be the dominant mode of speciation among parasites and parasitoids. More recent models have tended to invoke sexual selection (Kondrashov and Kondrashov 1999; Higashi et al. 1999). The whole question of sympatric (or quasi-sympatric) speciation has been under study in cichlids for some time by Axel Meyer and his colleagues, whose genomics studies find a variety of mechanisms which differ in different regions: sexual selection and selection in the trophic apparatus are identified in African rift valley lakes and Lake Victoria, while other mechanisms (such as color polymorphisms and breeding systems) are identified in the crater lakes of Nicaragua (see, e.g., Sanetra et al. 2009; Elmer and Meyer 2011; Fan et al. 2013).

Speciation, then, may occur by drift, natural selection, or sexual selection, with or without founder effect; it may involve intrinsic mechanisms such as chromosomal change or be simply a matter of divergence following allelic substitution and it may be allopatric, parapatric, or sympatric. To these mechanisms may be added speciation by hybridization (see below). We may infer the relative importance of these from phylogenetic studies (Barraclough et al. 1998; Groves 1989, 2012), although care must be taken to ensure that only sister groups are compared in such exercises.

How Long Does Speciation Take?

"Species flocks" in cichlid fish are monophyletic clades which are endemic to a single lake, such as Lake Nicaragua and Lake Managua in Central America, Lake Victoria, Lake Tanganyika and Lake Malawi in the Central African rift (see references to Meyer and colleagues, above), and Lake Barombi in Cameroon. In a very innovative study, McClune and Lovejoy (1998) used cytochrome b to compare differentiation, within-species flocks, among sympatric species to that among allopatric sets. The actual sequence divergence between sister species of fish was 2–8 %; this compares to that among geographic populations within given species, which was from 0 % to 5.6 %. The overlap between percent sequence divergence within species and that between species (allowing for the possibility that some species pairs were not sister species) was "time for speciation" (TFS); as the divergence associated with allopatric speciation was 2.0–5.6 % and that associated with sympatric speciation was 0–1.25 %, TFS was calculated to be 1–2.27 myr in allopatry, but anything from "instantaneous" to 0.77 myr in sympatry (using a cytochrome-b divergence rate of 2.5 % per million years). They admitted that these times could well be overestimates because of incomplete lineage sorting (which in some haplochromine cichlids "appears to be epidemic") and possible hybridization. The monophyletic swarm in Lake Victoria consists of 300 species; as the lake is only 12,400 years old, they calculate about 1,500 years per speciation event!

That speciation may take a very short period of time indeed and can be inferred from looking at changes that have occurred in taxa that have been introduced by human agency outside their natural ranges. Three examples have become especially well known:

- Mice (*Mus domesticus*) introduced apparently by the Vikings to the Faroe, Shetland, and Orkney Islands differ noticeably from the ancestral Scandinavian and/or British populations (Davis 1983). The mice of two of the Faroe Islands were described as a new subspecies by Degerbøl (1942), as was the hare whose history is similar.
- Australian wild rabbits differ appreciably from their parent population in the British Isles and are more and more different the further we go from Geelong (Victoria), the place where the small (a dozen or so) founding population was first introduced in 1859 (Taylor et al. 1977).
- In 1916, a pair of rock wallabies (*Petrogale penicillata*) was imported from New South Wales to Hawaii for a private zoo, but they escaped, and over 200 of their descendants now roam wild in the Ko'olau Range of Oahu. They are noticeably different in pelage, size, cranial characters, and body proportions from their ancestral population (Lazell 1980; Lazell et al. 1984).

These three examples are perhaps not actually speciation but certainly serve as examples of very rapid changes following the establishment of small founder populations. The Australian rabbit case also illustrates the principle of isolation-by-distance, meaning that populations that are more distant geographically may also be more distant genetically (the basis for clinal variation); considering the way rabbits disperse, not en masse but by forming small founder colonies, the cause of isolation-by-distance may, at least sometimes, be a progressive series of founder events.

Groves (1989:44–46) pointed out that the amount of heritable change following a founder event will vary in magnitude. Presumably, small gene frequency changes will be most frequent; the greater the degree of change, the less probable – but not vanishingly so. In the “sudden origins” model of Schwartz (1999), mutations of large potential effect, but recessive at first, accumulate in a population until their frequency reaches the point at which all at once they appear abundantly in homozygous state: similar, but not identical, to the way stasipatric speciation was envisaged by White (1978). If this is so, most founder events will not result in speciation, but some certainly will. The trick, of course, is to get these new species to survive when they come into sympatry with their parent species.

Is There Phyletic Speciation?

If founder effect is theoretically the most powerful way of generating new species, would speciation result if an entire population underwent the process (in other words, bottlenecking)? The “founder-flush” model of Carson (1975) relies on the fact that during the re-expansion phase after a population crash, there will be no density-dependent selection until carrying capacity is reached, so all kinds of zany mutants will survive to form new and potentially fit recombinations. Petry (1982) argued that this can apply to entire species. There are in fact real-world examples of this; some were described and discussed by Groves (1989:39–43). Consider: if this happened from time to time in a species with high visibility in the fossil record, it will mimic the appearance of anagenesis. We should be alert to the possibility of examples of punctuated equilibria without cladogenesis; there may be cases where rapid change in a fossil species occurs entirely in situ, rather than in small peripheral isolates. Gould (2002:779–780) was well aware of this; as he noted, cases of phyletic speciation might be distinguished from cases of allopatric speciation because the ancestral species is nowhere to be found.

Can We Detect Speciation Modes in the Fossil Record: Does Anagenesis Really Exist?

Groves (1989) pointed out that, if speciation really does drive evolution, we would expect to find that highly autapomorphic species have fossil records characterized by high rates of speciation, whereas their more plesiomorphic sister species would have had many fewer speciation episodes. The human species is highly autapomorphic, and indeed the fossil record depicts rampant speciation almost throughout; unfortunately, the case lacks a control, as the plesiomorphic sister group, the chimpanzee, has no fossil record whatever prior to the late Middle Pleistocene.

The reality of anagenesis has been vigorously defended by White (1995), and it is true that there are plenty of cases in the Plio-Pleistocene record where a pair of time-successive species (White’s example is in the suid genus *Kolpochoerus*) seem to merge into each other when fossils from intervening time zones become better known. Yet, as White (1995) notes, there are big problems which get in the way of a proper interpretation of the record: gaps are always there, key fossils are frustratingly incomplete, and examples of the same presumed species are not represented by comparable parts. A further problem is that "well-known cases" of anagenesis, which were plausible hypotheses in the state of knowledge of yesteryear, may call for reanalysis when they are looked at anew in the twenty-first century. A classic case of anagenetic gradualism was the inexorable onward-and-upward evolution of the East African Plio-Pleistocene elephant *Elephas recki*. More recently, Todd (2005, 2009) has maintained that all is not well with this icon of anagenesis, and a radical revision of the species (if it is one species) is in order.

How, in any case, would it work? Eldredge and Gould (1972) invited their colleagues to consider the implications of long-term sustained directional change – an environment exerting exactly the same selective pressures over perhaps millions of years. The most plausible scenario would be the Red Queen effect of Van Valen (1973), in which species themselves are constantly changing – usually degrading – their own environment and are forced to evolve continuously in order to track these changes. The Red Queen model incorporates everything from African elephants knocking down trees, and so destroying their own future food supply, to evolutionary arms races between lions and antelopes: everything, in other words, in which no evolutionary stable strategy is resolved. (The African elephant scenario is actually cyclical, although it is likely that natural climatic change does reset the cycles each time; such cases will therefore most likely be episodic, not continuous and sustained – see Cameron and Groves 2004.)

In cases of sustained trends, there is in any case an alternative: the effect hypothesis of Vrba (1980). In this model, new species are continually generated, and these are then subjected to the forces of selection; the ones which survive are those whose innovations happen to make them fitter in their particular habitat. At each round of speciation, this will occur, so that, if the environment has not changed much, an appearance of gradual directional change will result.

If it is difficult to test gradualism in the fossil record, how easy is it to test speciation? The answer is that, unless we catch it in the act, we can only infer it (from a pattern of stasis followed by sudden change); even then, the possibility of phyletic speciation (see above) cannot be ruled out. But there are a few cases where we have caught it in the act. The Morrisville cowpasture site, apparently documenting the evolution of a new species of trilobite, as described by Eldredge (1986, Chap. 3), may be one. Another, which appears to have survived all the criticism that was thrown at it, is the simultaneous eruption of new species in a dozen mollusk lineages in the Lake Turkana deposits (Williamson 1981). This latter case, as argued by Groves (1989), seems to flout the PE model because the new species were generated not by founder events in small isolates, but in huge populations. Yet it might instead shed light on mechanisms, because it occurred not instantaneously, as in cases that we have considered above, but over thousands of years, more as envisaged by Eldredge and Gould (1972) in their original paper; it might thus be explicable by a Kimura-type mechanism rather than by a Schwartz-type one.

Recently Groves (2012) suggested how one might go about deducing possible methods of speciation in the hominin fossil record. A case of simple dichopatric speciation, in which both of two sister species exhibit clear apomorphic states, might explain *Homo walkeri* (erstwhile *Paranthropus aethiopicus*) versus *H. africanus*, whereas the case of *H. africanus* versus *H. garhi* might indicate peripatric speciation in the case of the latter; yet the ubiquity of speciation by hybridization among living Primates warns us to be prepared for reticulation as well as divergence in the hominin record (see, e.g., *Homo ergaster and Its Contemporaries*, *The Species and Diversity of Australopiths* and *Analyzing Hominin Phylogeny* in this handbook).

Conclusion

This chapter has briefly surveyed the arguments over what is a species; the most nearly objective definition, the phylogenetic species concept (or phylogenetic delimitation method, in the model of de Queiroz (2007)), relies on genetic discontinuities and stands at the base of the "evolutionary species," which has a distinct evolutionary history and fate. How do species arise?

Gradualism (anagenetic change) is surprisingly hard to justify theoretically. If it could be demonstrated in the fossil record, this is something we would simply have to live with, but it is doubtful whether it can; at least one case (*Elephas recki*) that has been cited as a classic example of it has been found to need revision, and it is probably time to reexamine other supposed examples in fossil mammals, such as the African pig lineages.

Speciation is, in most cases, most likely a type of rapid cladogenesis; there is evidence to suggest that in some instances it may be very rapid indeed. It may be allopatric (peripatric), by a small population becoming isolated from the main body of the species, but stasipatric and even sympatric models are also plausible. Phyletic speciation, though it does not involve lineage splitting, also falls under the definition of speciation. In the fossil record, speciation would show up as a punctuation.

But, because a punctuation in most of the geological column – prior to the Neogene, anyway – is likely to take no more than "the duration of a bedding plane" (to quote Gould 2002:768), we are unlikely to catch it in the act very often. In most cases we have to fall back on inferring its operation. For example, a period of stasis followed by the sudden appearance of a new species is best explained by PE. And, if indeed speciation is the real focus of evolutionary change, then one expects to find evidence of much lineage splitting in the fossil record of highly autapomorphic species and very little in that of a plesiomorphic species; a proposition which is in need of testing in the future.

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Defining Hominidae
- ▶ Defining the Genus *Homo*
- ▶ Fossil Record of Miocene Hominoids

- ▶ Fossil Record of the Primates from the Paleocene to the Oligocene
- ▶ Historical Overview of Paleoanthropological Research
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ Modeling the Past: The Primatological Approach
- ▶ Molecular Evidence on Primate Origins and Evolution
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Quantitative Approaches to Phylogenetics
- ▶ The Species and Diversity of Australopiths

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Quantitative Approaches to Phylogenetics

Kaila E. Folinsbee, David C. Evans, Jörg Fröbisch, Daniel R. Brooks, and Linda A. Tsuji

Contents

K.E. Folinsbee (✉)
Department of Anthropology, Iowa State University, Ames, IA, USA
e-mail: kfolinsb@iastate.edu; positivist42@gmail.com

D.C. Evans
Department of Biology, University of Toronto at Mississauga, Mississauga, ON, Canada
e-mail: devans@utm.utoronto.ca

J. Fröbisch
Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt-Universität zu Berlin, Berlin, Germany
e-mail: joerg.froebisch@mfn-berlin.de

D.R. Brooks
Department of Ecology & Evolutionary Biology, University of Toronto, Toronto, ON, Canada
e-mail: dan.brooks@utoronto.ca; dnlbrooks@gmail.com

L.A. Tsuji
Department of Biology, University of Washington, Seattle, WA, USA
e-mail: latsuji@u.washington.edu; linda.tsuji@gmail.com

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Abstract

This chapter reviews Hennigian, maximum likelihood, and Bayesian approaches to quantitative phylogenetic analysis and discusses their strengths and weaknesses and protocols for assessing the relative robustness of one's results. Hennigian approaches are justified by the Darwinian concepts of phylogenetic conservatism and the cohesion of homologies, embodied in Hennig's Auxiliary Principle, and applied using outgroup comparisons. They use parsimony as an epistemological tool. Maximum likelihood and Bayesian likelihood approaches are based on an ontological use of parsimony, choosing the simplest model possible to explain the data. All methods identify the same core of unambiguous data in any given data set, producing highly similar results. Disagreements most often stem from insufficient numbers of unambiguous characters in one or more of the data types. If analyses based on different types of data or using different methods of phylogeny reconstruction, or some combination of both, do not produce the same results, more data are needed. New developments in the application of phylogenetic methods in paleoanthropology have resulted in major advances in the understanding of morphological character development, modes of speciation, and the recent evolutionary history of the human species.

Introduction

Formalized by Willi Hennig in 1950, phylogenetic systematics has emerged as a universal and transparent method for generating and evaluating evolutionary hypotheses. Over the last 50 years, it has developed into a research program ostensibly embraced by a majority of evolutionary biologists who are interested in exploring the patterns and processes of evolution. However, this apparent unity is misleading. As researchers from diverse fields began putting the theory and methods into practice, they approached their studies from different perspectives and used different types of data. This has generated a multitude of quantitative methods and research strategies, the efficiency and validity of which are fiercely debated in the literature.

These debates stem from the nature of phylogeny reconstruction. Unlike much of physics and chemistry (astronomy and astrophysics being notable exceptions), in which experiments in a hypothetico-deductive framework aim to be predictive with respect to spatiotemporally invariant laws, the reconstruction of phylogenies deals with a singular history and thus is descriptive and retrodictive. Attempts to infer causal processes for evolutionary patterns must be based not only on evolutionary patterns of relationships but also on corroboration from independent data (Wiley and Lieberman 2011; Brooks and McLennan 2002). Despite these obstacles, evolutionary biologists strive to provide as accurate an approximation of evolutionary history as possible.

Paleoanthropologists are especially concerned with the accurate reconstruction of primate evolution because fossils provide some of the most powerful evidence supporting evolution, the unifying theory of biology. More particularly, paleoanthropologists are the curators of information about the most fascinating evolutionary story of all, the story of *us*. As a critical part of evolutionary biology, paleoanthropology thus stands to benefit enormously from participation in phylogenetic research programs. Collaborating with researchers in diverse fields and exploring new methods will allow paleoanthropologists to refine their hypotheses and methods while placing them within the larger context of biotic evolution on this planet.

Fount of Stability and Confusion: A Synopsis of Parsimony in Systematics

The principle of parsimony (Latin *parcere*, to spare) is also known as the principle of simplicity. The principle is often connected to the English philosopher and Franciscan monk William of Ockham (ca. 1285–1349), who advocated the use of the principle so forcefully that it is also known as "Ockham's razor": *Pluralitas non est ponenda sine neccesitate* (plurality should not be posited without necessity) and *entia non sunt multiplicanda praeter necessitatem* (entities should not be multiplied unnecessarily). In this sense, the principle represents an epistemological tool or rule of thumb that favors theories or hypotheses that make the fewest unwarranted, or ad hoc, assumptions about the data from which they are derived. This does not necessarily imply that nature itself is parsimonious. Aristotle (350 BCE) articulated an ontological basis for the principle of parsimony, the postulate that "nature operates in the shortest way possible" and "the more limited, if adequate, is always preferable" (Charlesworth 1956). This sense of the principle postulates that nature is itself parsimonious in some manner. Phylogeneticists have used the term "parsimony" in both senses, resulting in much confusion and unnecessary conflict.

The most important concept introduced by Hennig (1950, 1966) was the stipulation that homology should be assumed in the absence of contradictory evidence. Although now known as Hennig's Auxiliary Principle, this concept lies at the foundation of evolutionary theory: "[p]erhaps the correct way of viewing the whole subject, would be, to look at the inheritance of every character whatever as the rule, and noninheritance as the anomaly" (Darwin 1859, p. 13), and "Mr. Waterhouse has remarked that, when a member belonging to one group of animals exhibits an affinity to a quite distinct group, this affinity in most cases is general and not special" (Darwin 1872, p. 409). Hennig's argumentation method is clearly intended to maximize hypotheses of homology and minimize hypothesis of homoplasy, which invokes the principle of parsimony by avoiding the assumption of unnecessary ad hoc hypotheses of parallelism. In the Hennigian system, if evolution were parsimonious, all traits would be logically consistent with the true phylogeny – there would be no conflicting relationships suggested by any set of traits, that is, there would be no homoplasy. The Auxiliary Principle implies that there will be conflicts in the data, which should be resolved in favor of the hypothesis postulating the fewest number of assumptions of multiple origins (homoplasy) over single origins (homology). Contemporary Hennigians assert that both the Auxiliary Principle and the use of parsimony are logical requirements of any attempt to reconstruct phylogeny; if one were to assert that all similarities were due to homoplasy, there would be no evidence of common descent and thus no evidence of evolution. Therefore, if one is going to study evolution, one must use a method that is capable of finding evidence of evolution. Likewise, if one is going to invoke the Auxiliary Principle, one must invoke it for all traits, thereby choosing the phylogenetic hypothesis that minimizes the total number of violations of the Auxiliary Principle for a given set of data. In this manner, the Auxiliary Principle is an epistemological tool practically synonymous with the principle of parsimony (Farris 1983; Wiley et al. 1991). Wiley (1981; Wiley and Lieberman 2011) suggested four main assumptions of phylogenetics: (1) evolution occurs and has occurred, documented by the characters of different species; (2) each species is a historically unique mosaic of plesiomorphic, synapomorphic, and autapomorphic traits; (3) prior to the analysis, it is unknown which characters are homologous and homoplasious; and (4) the phylogenetic relationships and relative or absolute rates of divergence are unknown. The presumption of homology embodied in Hennig's Auxiliary Principle is not an a priori assumption in the sense of a formal model, because the method is designed in part to recognize all mistakenly presumed homologies as homoplasies.

Edwards and Cavalli-Sforza (1963) reconstructed a tree of extant human populations based on frequencies of blood-group alleles, using an approach they developed and called the "Method of Minimum Evolution." Their studies originally aimed to present a maximum likelihood method for phylogeny reconstruction, but their algorithm for a likelihood approach did not work. Edwards (1996, p. 83) later emphasized that "[t]he idea of the method of minimum evolution arose solely from a desire to approximate the maximum likelihood solution," that is, from a maximum likelihood model based on the assumption that evolution has been parsimonious. Felsenstein (2004, p. 127) characterized the method of minimum evolution as a parsimony method while at the same time not seeing a direct connection between Hennig's Auxiliary Principle and the principle of parsimony, e.g., "[i]t is not obvious how to get from this 'auxiliary principle' to the parsimony criterion" (Felsenstein 2004, p. 138). This reveals that for Felsenstein and like-minded phylogeneticists, parsimony is an ontological issue, whereas Hennigians see it as an epistemological issue.

There are two critical distinctions between these positions. The ontological perspective on parsimony requires first that evolution be parsimonious in some manner, usually as defined by certain assumptions and parameters of a model, and second that the resulting phylogenetic hypothesis be accepted as true so long as the model is accepted as true. Practitioners are thus preoccupied with the accuracy of their results and believe it is possible to develop means by which their preferred hypotheses can be verified with respect to the true phylogeny. The Hennigian or epistemological use of parsimony does not imply that the evolutionary process itself is parsimonious. In fact, it suggests that evolution has been so complex that conflicts will always be found in the data, which will require the use of a logical decision-making principle to resolve. An important corollary of this perspective is that there need be no necessary connection between the most parsimonious hypothesis and truth. Practitioners are thus preoccupied with the empirical robustness of their results. The expectation is that if the most parsimonious hypothesis is not true, the accumulation of additional data will force phylogeneticists to abandon it in favor of a new most parsimonious hypothesis; they do not believe that their hypotheses can be verified, but do believe that they can use new data to falsify all or parts of previous hypotheses. Phylogeny reconstruction is thus an open-ended process involving a potentially endless search for information. If, at some point in the future, the accumulation of data has led to a situation in which the phylogenetic hypothesis for a given group is no longer changing with the addition of new data, Hennigians may express the belief that the hypothesis has approached the truth as closely as possible, but in principle it is never appropriate for a Hennigian to claim to have the true phylogeny. Hennigians do feel justified in claiming that they have the most robust hypothesis possible for any set of data.

Today numerous quantitative methods for reconstructing phylogenetic trees are applied to multiple kinds of characters. These methods can be divided into two main types, commonly called parsimony (invoking epistemological parsimony) and likelihood (invoking ontological parsimony) approaches.

Epistemological Parsimony: The Wagner Algorithm

In September 1965, two seminal articles on phylogeny and parsimony appeared. Wilson (1965) introduced a "consistency test for phylogenies based on contemporaneous species." His null hypothesis was that all characters that are used for a phylogenetic analysis are unique and unreversed. In order to pass Wilson's consistency test, the taxa defined by these characters must be nested, and these nested conditions must persist as new species are added to the tree. Colless (1966) was concerned that more than one cladogram might pass the consistency test, that a polyphyletic character state might mistakenly be regarded as unique and unreversed, and that the taxa are in the first place grouped on the basis of similarities. Wilson (1967, p. 104) asserted that his consistency test was internally sound but that he shared one of Colless' main concerns, which "is the lack of efficient methods for selecting the character states."

In the second article, Camin and Sokal (1965) presented the first algorithm for applying the parsimony criterion to phylogenetics and first applied the term "parsimony" to a method of phylogenetic inference. They used a group of imaginary animals (Caminalcules) possessing a number of morphological characters that could change according to particular rules. Thus, the "true phylogenetic tree" was known and could be compared to trees that were achieved by different methodologies. Camin and Sokal (1965) found that the trees that most closely resembled the "true phylogeny" required the least number of changes in the morphological characters, which seems to invoke an epistemological use of parsimony. However, they claimed that their technique examined "the possibility of reconstructing cladistics by the principle of evolutionary parsimony" (p. 312), saying that "the correctness of our approach depends on the assumption that nature is, indeed, parsimonious" (pp. 323–324), an appeal to ontological parsimony. Significantly, Camin and Sokal produced a computer program implementing their method, demonstrating for the first time that quantitative phylogenetic analysis could be performed on as objective a basis as phenetics, thereby undermining one of the strongest arguments in favor of phenetics over evolutionary approaches to systematics (Sokal and Sneath 1963). Their algorithm was, however, unwieldy and inefficient for larger data sets and was never fully adopted nor effectively programmed and made available for widespread use.

Soon afterward, Kluge and Farris (1969; also Farris 1970) presented a new algorithm for reconstructing phylogenetic trees as well as searching among several trees for the most parsimonious tree for a given data set. They named their method "Wagner parsimony" in honor of W. H. Wagner, who formalized an older approach (Mitchell 1901, 1905) called the groundplan-divergence method (Wagner 1952, 1961, 1969, 1980), which formed the basis for Kluge and Farris' algorithm. Kluge and Farris (1969) also discussed explicitly their perspective that the use of the parsimony criterion did not assume that evolution itself is parsimonious, clearly invoking an epistemological use of the principle.

The Wagner Algorithm

The first Wagner algorithm [in later papers termed the "simple Wagner algorithm" of Kluge and Farris (1969)] utilizes a method that minimizes the Manhattan distance between members of a set of taxa via the creation of hypothetical taxonomic units. This initial algorithm required the selection of an ancestral taxon, but in 1970 Farris concluded that it was unnecessary to have an ancestor from which to begin the construction of the tree (Farris 1970). He observed that the choice of ancestor of a given group of taxa changed the topology of the tree. Since the "simple" algorithm did not impose directionality to the evolution of the group, he reasoned that the choice of ancestor is not crucial. Parsimony assumes the least about the way evolution works, so choosing one taxon as an ancestor would be an assumption about the status of that taxon. Farris thus argued that a rootless network would reduce the dependency of the form of the tree on the ancestor. For the creation of networks, he used a method for creating networks that minimized the length of the intervals between taxa (symbolized by nodes), using the shortest network connections method of Prim (1957; Sokal and Sneath 1963). Farris differentiated his use of this method from previous phenetic applications by its use of shared, derived characters and also by the evolutionary implications of the method.

This new Wagner algorithm produces a network, rather than a tree, and does not assume that any of the taxa are ancestral. Farris suggested that the network could be converted into a phylogenetic tree by rooting it at one of the taxa within the tree or an interval within the network. Completing the process of constructing phylogenies using this method requires that the characters be optimized onto the tree.

The earliest programs implementing the Wagner algorithm did not necessarily find the most parsimonious tree for large data sets. The program needed to run multiple times and have a method of comparison in order to determine whether it has indeed found the shortest tree or if there were multiple equally parsimonious trees. In a large matrix, examining every possible tree could require an enormous amount of computer time, and thus it became necessary to develop heuristic methods to try to find the shortest tree. Today's parsimony programs, such as those in PAUP, Hennig86, NONA, and TNT, use a variety of heuristic algorithms to rerun the data to attempt to ensure that the most parsimonious tree or trees are found. For small numbers of taxa and characters, the Branch and Bound algorithm (Hendy and Penny 1982), which guarantees finding the shortest tree, or the Exhaustive Search option, which enumerates all possible trees, can be employed.

As phylogeneticists began to analyze increasingly larger and more complicated data sets, the shortcomings of the original computer programs became evident. In the decade following Farris' (1970) contribution, a number of algorithms were developed and incorporated into the existing programs as alternatives to Wagner parsimony. These differed primarily in their assumptions and restrictions regarding character evolution and are discussed in more detail by Wiley et al. (1991).

The first iteration of the Wagner algorithm did not take into account multistate characters, and therefore technically it was not possible to have unordered states, since polarized binary characters are automatically ordered. Initially, before more variations were developed for the algorithm, it was suggested that all multiple character states be divided into multiple binary characters [e.g., a single multistate transformation series of an imaginary character (absent (0), short (1), long (2)) would be divided into two separate characters (absent (0) and present (1) and short (0) and long (1))]. Current algorithms allow for multistate transformation series and allow characters to be run either polarized or unpolarized, and either ordered or unordered, at the discretion of the user. Again, the advantage of phylogenetic methodology is that these decisions are transparent (if they are reported) and repeatable; with the same data set, anyone can rerun an analysis using the same settings to check the reliability of the analysis or change the settings to see if the results are different.

Whichever algorithm is used to build a tree, in most cases some characters will not be decisive at every node (Farris 1970). It is therefore important for the purpose of studying character evolution to be able to optimize characters on a tree. There are two types of optimization, ACCTRAN (Farris 1970; Wiley et al. 1991) and DELTRAN (Swofford and Maddison 1987; Wiley et al. 1991). The ACCTRAN setting accelerates the transformation of a character on a tree, making the derived state evolve earlier, or toward the root. This is equivalent to preferring parallelisms to reversals as long as the choice does not affect the tree length. DELTRAN delays the transformation of a character on a tree, essentially choosing reversals over parallelisms when they are equally parsimonious (Wiley et al. 1991). When there are no equally parsimonious alternatives, both ACCTRAN and DELTRAN will provide the same result (Figs. 1 and 2).

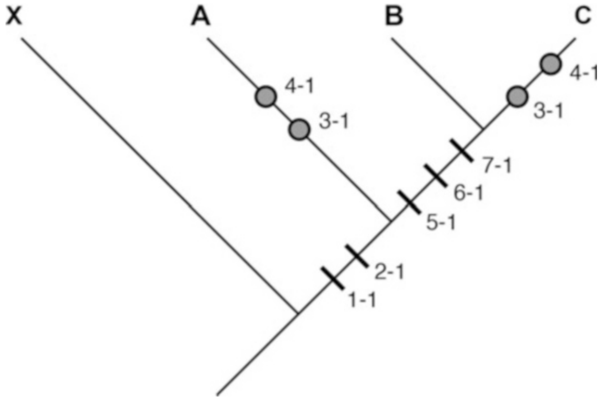

Fig. 1 ACCTRAN tree (length = 9 steps) (Redrawn and modified from Wiley et al. (1991). Characters 3-1 and 4-1 evolve in parallel in taxa A and C)

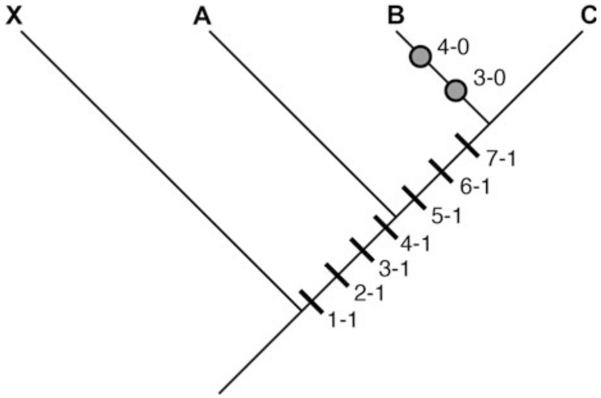

Fig. 2 DELTRAN tree (length = 9 steps) (Redrawn and modified from Wiley et al. (1991). Characters 3-1 and 4-1 are secondarily lost in taxon B)

Development of Outgroup Comparison

As noted above, the Wagner algorithm generates a minimum-length network (sometimes called an "unrooted tree"). In order to convert a Wagner network into a phylogenetic tree, the network must be rooted in some manner. Increasingly, published studies convert the network into a tree by rooting it with an arbitrarily chosen single taxon not included in the group being analyzed (called the ingroup). This protocol should not be mistaken for the method of outgroup comparisons that emerged in phylogenetics during the 1970s. The distinction is slight but significant and must be understood in light of Hennig's perspective on the issue of ancestors.

Hennig objected strongly to the notion that phylogeny reconstruction could be achieved by reconstructing a series of archetypal ancestors from which particular descendant species could be derived. His position was that each species was a unique mosaic of plesiomorphic and apomorphic traits. Archetypes, defined as ancestral species exhibiting only plesiomorphic traits, thus did not exist; therefore, no single taxon could be used to determine the plesiomorphic and apomorphic traits for any analysis. Or, using current jargon, rooting a network with a single outgroup taxon is sufficiently robust in the Hennigian system only if that taxon is the archetype ancestor of the ingroup, something the Hennigian system disavows.

As can be seen from the discussion above, the early development of the Wagner algorithm was not informed directly by Hennigian reasoning. Rather, it relied on the groundplan-divergence method, based on a priori recognition of an archetypal ancestor. When Farris (1970) abandoned the a priori reliance on an ancestor, the Wagner algorithm reverted to a method for producing an unrooted network. Lundberg (1972) made a significant contribution to linking the results of Wagner analyses with Hennigian analyses, by differentiating ancestors from outgroups.

Lundberg developed a method to determine an ancestor from within a network from the data within that same network. He opined that the structure of a network makes certain character states more likely to be ancestral, helping to determine which interval should form the root of the tree of a parsimony-optimized network. The transition of emphasis from searching for ancestors to identifying outgroups was critical in linking Wagner with Hennig. However, the idea that similarity in traits even among distantly related species was due to homology (i.e., plesiomorphy) rather than independent evolution (homoplasy) was established before the development of Hennigian systematics (e.g., Darwin 1872).

Despite the fact that the connection between outgroups and the Auxiliary Principle had been around for a long time, there was no codification until the late 1970s. Engelmann and Wiley (1977) were the first to provide a rationale for outgroup comparisons. They pointed out that the reference to species outside the ingroup permits a researcher to distinguish traits that truly conflict with phylogeny (homoplasies) from those that only appear to conflict (plesiomorphies). This in turn creates the possibility that phylogenetic analysis could become testable, at least with respect to Darwinian concepts. Watrous and Wheeler (1981) expanded on this idea, suggesting a number of rules to determine ancestral states for each independent character on the basis of comparisons with an outgroup taxon. The first algorithm to determine ingroup relationships with reference to multiple outgroups was presented by Maddison et al. (1984), who showed that the most robust outgroup comparisons relied on two or more paraphyletic outgroups. This algorithm is incorporated in the program PAUP to root networks when outgroups are specified.

Linking the Auxiliary Principle to outgroup comparisons thus provides a connection, through the Auxiliary Principle, between outgroup comparisons and parsimony. It is the use of outgroups to root the shortest network that makes the Wagner algorithm Hennigian, accounting for high degrees of consistency between Wagner algorithm, groundplan-divergence method, and Hennig argumentation of the same data.

Evaluating the Robustness of a Parsimony Analysis

Character Evaluation

Hennigian phylogeneticists are preoccupied with assessing the empirical robustness of their results. There are various methods available to accomplish this goal. These “goodness of fit” measures are useful indicators of the degree of internal conflict among the data (characters) used. Measuring the robustness of the characters and knowing how they behave over the tree topology is one useful approach (Wiley and Lieberman 2011).

The simplest summary statistic is the *tree length*; it is merely the number of steps required to produce a particular topology, and it is calculated by adding the number of character changes over the tree (Wiley et al. 1991). Parsimony analysis chooses the tree or trees with the shortest overall length given a set of characters.

Consistency indices (Kluge and Farris 1969) attempt to quantify the amount of homoplasy on a particular tree. The original form of the *consistency index* (CI) is the ratio of the total number of apomorphic states to the tree length. A high CI indicates there is little homoplasy (i.e., the tree length approaches the minimum number of steps required) and a low CI indicates there is a high degree of homoplasy. This measure is independent of a particular data set and thus can be used to compare trees produced by different data. However, the CI can be inflated by autapomorphies, which do not represent tests of relationships and thus are not informative with respect to the robustness of the tree. Farris (1989) therefore proposed the *rescaled consistency index* (RC). The RC is an adjusted version of the CI with the influence of characters that do not change the fit of the tree (e.g., autapomorphies) removed. It still gives a relative measure of the degree of homoplasy on a particular tree topology.

Tree Evaluation

A second type of evaluation assesses the robustness of the tree topology itself. *Decay analysis* (Bremer 1988) determines the number of steps required to collapse nodes. To perform a decay analysis, tree length is increased by successive steps. This shows how many trees exist that are one or more steps longer than the most parsimonious tree (MPT); if there are a few trees of similar length to the MPT, but with different topologies, the MPT is more likely to be accurate. A decay analysis will also reveal how many added steps it takes to collapse individual nodes and which specific characters influence those nodes. This in turn allows a test whether a set of functionally correlated characters influences a particular node.

Hennigian analysis of a data set may produce more than one tree with the same number of fewest possible steps, a phenomenon known as *multiple most parsimonious trees*. With a large number of taxa and characters, especially if they contain large amounts of homoplasy or missing data, parsimony frequently generates multiple MPTs. In these cases, it is not possible to designate a single preferred tree; however, it is possible to generate a variety of *consensus trees* to delineate similarities in topologies of different MPTs (Adams 1972). Consensus techniques are useful as visual summaries of points of agreement or logical consistency between MPTs, but they are not phylogenies, and they are not equivalent to what is produced by phylogenetic analysis of a data matrix.

Bootstrap and *jackknife* analyses attempt to estimate the degree of sampling error in the original data set, by attempting to place confidence intervals on phylogenies by making inferences about the variability in the data set. Bootstrapping (Felsenstein 1985a) samples the data set with replacement; that is, it allows for some characters to be sampled more than once, and for some not to be included at all, and constructs a new data set with the same number of characters. PAUP* (Swofford 1998) and other programs construct a series of these and build a majority-rule consensus tree that summarizes the results of the resampled data. The number of times a particular group is included in the set of trees that form the consensus is an estimate of the reality of that group in that the process has measured the amount of variation between the newly sampled data sets. The bootstrap is, then, a measure of the confidence placed in each node of the tree, like the decay index. Felsenstein (1985a) suggested that a bootstrap value of 95 % or greater offers statistically significant support for a clade.

There are a number of caveats to consider before placing too much faith in the numbers generated by this analysis. Since the bootstrap measures the variation in one set of data, it cannot be used to compare trees built from different data sets. Felsenstein (1985a) stipulated that a bootstrap assumes characters are independent and equally distributed. He was explicit that the bootstrap indicates *repeatability* of an analysis given the data and should not imply the phylogenetic *accuracy* of a tree. It may also be affected by biases such as long-branch attraction (Swofford 1998).

The *jackknife* is another mode of evaluation, similar to the bootstrap in that it estimates variability in the data set. It is a procedure to resample data by deleting a certain number of characters [either half (Felsenstein 1985a) or another fraction (Farris et al. 1996)] and resampling the data without allowing characters to be duplicated. Characters are randomly and independently deleted from the original matrix to create a new “resampled” matrix, and like the bootstrap, many matrices are produced and the results are compiled into a consensus tree.

Ontological Parsimony: Maximum Likelihood and Bayesian Likelihood Approaches

A Precis of Maximum Likelihood in Phylogenetics

Microbiology made significant progress in the late 1950s when the first proteins were sequenced. Molecular data were soon recognized to be an important source of phylogenetic information useful in inferring evolutionary relationships (Sneath and Sokal 1973; Neyman 1974). Edwards and Cavalli-Sforza (1963) first explored the idea that likelihood could be applied to phylogeny reconstruction. Cavalli-Sforza and Edwards (1967) later described a likelihood method for phylogenetic inference using blood-group allele frequency data in human populations. Neyman (1974) was the first to apply likelihood analysis to nucleotide sequences and presciently suggested that this approach might become important in the future. Farris (1973) and Felsenstein (1973) published likelihood algorithms for phylogeny reconstruction; however, computational problems continued to limit a likelihood method for phylogenetic inference to the theoretical rather than practically operational. Felsenstein (1981) introduced the first computationally efficient maximum likelihood algorithm for discrete character nucleotide sequence data. Just as the Wagner algorithm became the algorithm of choice for quantitative Hennigian analyses, nearly all phylogenetic applications of maximum likelihood are adapted from Felsenstein's early work. Since then, maximum likelihood methods have become increasingly popular in phylogenetic studies (Swofford et al. 1996; Huelsenbeck and Crandall 1997; Felsenstein 2004). These approaches are most commonly used in molecular phylogenetics (Swofford et al. 1996; Huelsenbeck and Crandall 1997; Huelsenbeck et al. 2002; Ronquist 2004), but morphology-based and combined likelihood and Bayesian methods are becoming more widely used (Lewis 2001; Ronquist 2004; O'Leary and Gatesy 2008; Wiens 2009; Wiens et al. 2010). Probably due to the relative ease of acquiring molecular sequence data, molecular phylogenies have been published at a far greater rate in recent years than phylogenies based on morphological data. However, morphological characters remain the only source of data for virtually all extinct taxa.

Likelihood Methods

Several methods for inferring phylogenies from nucleotide sequence data are available, resulting in an often-heated debate among evolutionary biologists over the "best" way to approach phylogeny reconstruction (Goldman 1990; Penny et al. 1992; Swofford et al. 1996; Huelsenbeck and Crandall 1997; Steel and Penny 2000). Maximum likelihood methods evaluate a hypothesis of evolutionary relationships using a presumed model of the evolutionary process and evaluate the probability that it would give rise to the observed data, which are typically DNA sequences of the terminal taxa (Felsenstein 1973, 1981, 2004; Swofford et al. 1996; Huelsenbeck and Crandall 1997). Phylogenetic-likelihood approaches use maximum average likelihood, a form of maximum relative likelihood (except Farris 1973, which adopted evolutionary pathway likelihood), and only this form applies to the discussion below (Steel and Penny 2000).

The likelihood of a hypothesis (Fisher 1922) is the probability, P, of the data (D), given the hypothesis (H):

$$L = P(H|D)$$

The likelihood of a parameter is proportional to the probability of the data, and it gives a function that usually, but not always, has a single maximum value, which Fisher called the maximum likelihood. The likelihood equation above the hypothesis, which is assumed to be true in the likelihood formulation above.

Likelihoods are calculated for different possible tree topologies, given the data and assuming a particular model of molecular evolution (Felsenstein 1973, 1981, 2004; Swofford et al. 1996). In the likelihood equation above the hypothesis, H, contains three distinct parts: (1) a mechanism or model of sequence evolution, (2) a tree or a hypothesis of relationships, and (3) branch lengths (Penny et al. 1992). For a given data set, likelihoods are calculated for each of the possible tree topologies or a sample of them, and the tree topology with the highest overall likelihood is the preferred phylogenetic hypothesis. The number of possible tree topologies increases with the number of terminal taxa included in the analysis. This can be computationally laborious if the data set is large and especially if the maximum likelihood model uses rooted trees in its calculus. However, the most general and most commonly used models in molecular analyses are time reversible (Rodriguez et al. 1990; Swofford et al. 1996). With a time-reversible model, the probability of character state change from state *i* to state *j* is the same as the probability of state change from state *j* to state *i* (Felsenstein 1981). Under this condition, the likelihood of the tree does not depend on the position of the root, and the use of unrooted networks greatly reduces the total number of trees to be evaluated and decreases computation time (Rodriguez et al. 1990; Swofford et al. 1996). For a detailed discussion of likelihood methods, see Felsenstein (2004).

Models of Molecular Evolution

Models in likelihood phylogenetics are tools that aid in the estimation of tree topology (Kelchner and Thomas 2007). Likelihood analyses involve similar assumptions about the evolutionary process as other methods, including that evolution occurs in a branching pattern and is independent in different lineages (Swofford et al. 1996). The probability of a particular combination of character states at the internal nodes of the unrooted network is calculated using a specified model of molecular evolution, which requires further assumptions about the nucleotide substitution process, including that sequence evolution can be modeled as a random, or stochastic, process (Rodriguez et al. 1990). Substitution models are typically based on a homogeneous Markov process (Rodriguez et al. 1990;

Swofford et al. 1996) that assumes that the probability of a state change at one site does not depend on the history of that site and that probabilities of substitution do not change significantly in different parts of the tree (Felsenstein 1981, 2004; Swofford et al. 1996).

Models employed in likelihood analyses make explicit assumptions regarding sequence evolution, the number of which depends on the particular model of sequence evolution used in the particular analysis (Swofford et al. 1996). The simplest model, Jukes-Cantor, assumes that all base substitutions are equally likely (i.e., all rate parameters are equal) and that the base frequency parameters are equal. The general time-reversible model (GTR) is the most general stochastic model of nucleotide substitution and is the model most frequently used in the phylogenetic literature (Kelchner and Thomas 2007). It models base substitution as a random Markov process in which substitution rates are independent among sites, constant in time, and equal in two lineages and the ancestral sequence base frequencies represent the equilibrium frequencies (Rodriguez et al. 1990). The GTR model has a maximum of 12 different substitution rates (estimated from the data and using the aforementioned assumptions in their calculus) and at least seven parameters (Rodriguez et al. 1990). Because of its greater complexity, nearly all models can be considered special cases of the GTR model when it is restricted accordingly (Rodriguez et al. 1990).

Characters and their associated probabilities are not independent quantities but are assumed to be in the calculus of the method (Felsenstein 1973, 1981; Rodriguez et al. 1990; Swofford et al. 1996). The non-independence of site change probabilities may be one factor responsible for the fact that the total likelihood of the universe of possible trees does not sum to unity (Felsenstein 1981). The true probabilities for character changes should be calculated on an individual basis, because they are connected with unique and historically contingent events (see below) as pointed out by Farris (1973). But this is clearly impossible, as it not only requires knowledge of the true history before undertaking an analysis, it also requires an objective and consistent way of determining the probability of a novel, context-specific evolutionary event (see below, Farris 1973). It would also be computationally impossible (Felsenstein 1973, 1981; Siddall and Kluge 1997). As currently and commonly employed in phylogenetic maximum likelihood methods, frequency probability theory is technically violated (Yang 1996; Siddall and Kluge 1997).

Choosing a Model: More Ontological Parsimony

The choice of an appropriate model is a critical aspect of a phylogenetic-likelihood analysis. Posada and Crandall (1998) argued that the use of their ModelTest program makes selection of the model objective. There are many models of molecular evolution, and the determination of which to use can significantly influence the results of an analysis. Models range in complexity from the relatively simple Jukes-Cantor model through the most complex GTR model. The overall likelihood score of a tree increases with increasing complexity of the model, but the accuracy of the model decreases due to the increased number of estimated parameters (Huelsenbeck and Rannala 1997a). The program conducts pairwise comparison of the maximum likelihood trees generated under each model using hierarchical-likelihood ratio tests (Huelsenbeck and Crandall 1997; Huelsenbeck and Rannala 1997a; Posada and Crandall 1998). When no statistically significant difference between two trees is found, the simplest model is selected. Model selection based on the *relative* likelihood values is an ontological appeal to the principle of parsimony, because choosing the least complex explanation of the data rules out the possibility that evolution proceeded in a more complex manner (Huelsenbeck and Rannala 1997a).

Criticisms of the Models

Many criticisms of maximum likelihood methods are directed at this a priori dependence on a model. Evolutionary realism of the models employed in likelihood analyses is often compromised by approximations that are designed to improve the computational efficiency of the algorithms. For example, Lockhart et al. (1994) suggested that a modified GTR model, in which time reversibility is relaxed, across site rate variation is considered and the nucleotide compositional frequencies are flexible, allow more evolutionary “freedom” than any other model, and best consider the historical ambiguity and contingency of the evolutionary process. They suggested that this complex, parameter-rich, and computationally intensive model should be logically preferred over all other models, if inferring phylogeny using the most realistic conception of evolution (i.e., evolution is complex) is the goal of the analysis. The problem is that relaxing the time-reversibility assumption introduces the need for rooted trees and is accompanied by additional computational problems (Swofford et al. 1996). Relaxing the assumption that rates are equal across all sites can be accomplished by adding another relative rate parameter to the matrix, which commonly involves modeling rate heterogeneity using the gamma distribution (Swofford et al. 1996). If this distribution is modeled as continuous (as it should be), it again becomes computationally laborious, and a discrete distribution typically serves as a computationally more efficient approximation (Swofford et al. 1996).

The likelihood method also requires that numerous parameters be approximated using the data and relies heavily on the frequency parameters that are taken directly from the observed sequences (Swofford et al. 1996). In this sense, likelihood methods assume that the processes that maintain systems today were persistent throughout the entire evolutionary history of the clade being investigated (Brooks and McLennan 2002). Siddall and Kluge (1997) and Lockhart et al. (1994) provide an empirical example where the nucleotide frequencies are very different across the terminal taxa, proving that the assumption of equilibrium base frequencies is not at all tenable and that the assumption of such can affect likelihood phylogenies. When the model is insufficient or inappropriate, appeals to statistical consistency are rendered moot (Siddall and Kluge 1997).

Criticisms of the Method

Phylogenetic applications of likelihood rely on two fundamental assumptions that evolution is independent in different lineages as well as independent in different sites for a given tree, which are essential for the probability calculations on which the method is based (Felsenstein 1981, 2004; Rodriguez et al. 1990; Swofford et al. 1996). Both assumptions are methodologically problematic because they are unrealistic and/or violated in the calculus (Siddall and Kluge 1997; Huelsenbeck and Nielsen 1999), but likelihoodists appeal to simulations to argue that the method is generally robust to violations of these assumptions (Yang 1994; Swofford et al. 1996). It is also assumed that the same stochastic process of substitution applies in all lineages (Felsenstein 1981).

Many researchers advocate a model-based maximum likelihood approach (Felsenstein 1978, 1981, 2004; Goldman 1990; Penny et al. 1992; Yang 1996; Huelsenbeck and Rannala 1997a; de Queiroz and Poe 2003). Others (Siddall and Kluge 1997; Kluge 2001; Goloboff 2003) cite operational and philosophical problems of likelihood methods and discourage its use in phylogenetic inference.

Likelihood methods rely on a specified model of sequence evolution to infer phylogenetic relationships. This is an inductive approach, as the assumptions of the model are clearly deterministic to the result of the analysis. In phylogenetic-likelihood analyses, like all inductive approaches in science, all interpretations of the results come with the caveat "if the model is true, then. . .." Because likelihood is inductive estimation of phylogeny, particular caution must be taken in interpreting the results and to avoid circularity. ModelTest reveals which of the models best fit the data, but how can the validity of the model itself be independently tested? Testing of the validity of models, although it has been recognized as important (Goldman 1990), is rarely done in practice (Siddall and Kluge 1997). In a hypothetico-deductive framework, the assumptions of the method are background and not deterministic to the result. Only the observable data is considered, maximizing the explanatory power of the hypothesis and minimizing ad hoc hypotheses (i.e., hypotheses that confide in "nonobservables," such as long branches in a likelihood framework). It has been argued that many of the simple assumptions of the evolutionary models (i.e., the frequency of transitions versus transversions) constitute grounded knowledge about the process of molecular evolution and therefore is an acceptable background assumption. However, the maximum likelihood approach suggests that this is and has always been the case throughout the evolutionary history of a group, which is a problematic assertion with respect to the historically contingent nature of the evolutionary process (Siddall and Kluge 1997).

Likelihood methods are based on frequency probability theory. Frequency probability is concerned with prediction of future events (Fisher 1922). The aim of phylogenetic systematics is to discover the unique evolutionary history of a group of organisms or to elucidate its past (Kluge 1997). A species must be considered a historical entity (Kluge 1990), and evolutionary transformations are unique and spatiotemporally restricted historical events (Siddall and Kluge 1997). Frequency-probability-based methods of phylogenetic inference, such as maximum likelihood, apply frequency probability to a *historical singularity*, which is outside of the realm of future-predictive probability theory (Siddall and Kluge 1997). As noted above, likelihood methods assign all trees a nonzero probability, but in reality one tree has a probability of 1.0, and others have a probability of zero. One must be cognizant that maximum likelihood inference of phylogenies is philosophically unsound because it employs frequency probability theory to estimate a nonprobabilistic phenomenon.

Bayesian Likelihood

In spite of these numerous criticisms, most molecular phylogeneticists prefer likelihood approaches because sequence evolution can be explicitly incorporated into the analysis. One of the more popular iterations of likelihood is Bayesian analysis (Huelsenbeck et al. 2002).

Bayesian methods calculate the posterior probabilities of phylogenetic hypotheses (trees) using a version of Bayes' theorem in which the likelihood of the tree and the prior probability of the tree are considered (Huelsenbeck et al. 2002). Huelsenbeck et al. (2001, 2002) provide an excellent review of the history and mechanics of Bayesian inference methods in phylogeny.

Reverend Thomas Bayes, living in the early half of the eighteenth century, was an English mathematician who was interested in the concept of using a priori knowledge to predict future events. His paper, "An Essay Towards Solving a Problem in the Doctrine of Chances," published 2 years after Bayes' death in 1761, introduced what would become known as Bayes' theorem (Barnard and Bayes 1958).

$$P(H|D) = \frac{P(D|H)xP(H)}{P(D)}$$

The posterior probability [P(H|D)] is the probability of the hypothesis given the observations or data (D). Note that this is different from likelihood, which is the probability of the data given the hypothesis. However, the likelihood, P(D|H), is a parameter in the calculation of the posterior probability. P(H) is the *prior* probability of the hypothesis before the observation, data, or analysis and reflects the original beliefs regarding the problem. The probability of the hypothesis is updated to take into account the observations, and Bayes' theorem describes the relationship between the prior and posterior probabilities. It was not until the latter half of the twentieth century that Bayes' ideas would be applied to the inference of phylogenies. Felsenstein (1968) briefly discussed Bayesian ideas as they could apply to phylogeny reconstruction in his Ph.D. thesis, but the statistical and computational framework with which to derive reliable approximations of posterior probabilities was not available at the time (Huelsenbeck et al. 2002). In 1996, three independent groups introduced Bayesian methods similar to those currently in use (Li 1996;

Mau 1996). Bayesian methods to estimate ancestral character states have also been developed (Pagel et al. 2004; Ronquist 2004).

Bayesian phylogenetic inference evaluates phylogenetic hypotheses with the posterior probabilities of trees. The posterior probability of each tree is calculated using the following Bayes-based equation, where the tree topology (including branch lengths) is the hypothesis, and the data are typically molecular sequences of the terminal taxa in the analysis.

$$P(Tree|Data) = \frac{P(Data|Tree)xP(Tree)}{P(Data)}$$

The likelihood parameter, P(Data|Tree), is calculated using the same general methodology and same models of molecular evolution described above for the maximum likelihood approach. However, one major difference between Bayesian and maximum likelihood methods is that Bayesian likelihood calculation not only involves summation over all possible combinations of model parameters and branch lengths but also includes a prior probability density distribution of these latter variables (Huelsenbeck et al. 2002). The prior probability of the tree, P(Tree), is usually considered to be equal for all trees a priori (Huelsenbeck et al. 2001). The use of equal priors implies that no particular topology is preferred over any other a priori and eliminates the sometimes difficult task of calculation of complex priors when hypotheses vary with respect to their preconceived probabilities. However, the prior for any given tree or set of trees can be set to reflect researcher experience, the results of previous analyses, or taxonomy (Huelsenbeck et al. 2002). The denominator, simplified here as P(Data), is a normalizing factor that involves summation over all trees (Huelsenbeck et al. 2002). The posterior probability, P(Tree|Data), can be viewed simply as the probability that the tree is “correct,” *given* the data and the priors, and that the model of character change used in the likelihood calculation is correct (Huelsenbeck et al. 2002). There are several ways to present the results of a Bayesian analysis. The tree with the maximum posterior probability can be selected as the preferred phylogenetic hypothesis; this is also known as the MAP, maximum a posteriori, estimation of phylogeny (Huelsenbeck et al. 2002). Another method is to construct a 95 % credibility consensus tree by starting with the MAP and consecutively adding the next most probable trees until the probabilities total 0.95 (Huelsenbeck et al. 2001, 2002). The method preferred by Huelsenbeck et al. (2002) is to present a summary of the results on the MAP or another consensus tree, as is typically done with bootstrap.

Calculation of the posterior probability of a tree is computationally expensive, because it involves summation over all possible trees, and for each tree requires integration over all possible permutations of branch lengths and substitution-model parameters (Huelsenbeck et al. 2001, 2002). This is not possible in most practical applications due to computational and time constraints and requires that posterior probabilities be approximated (Huelsenbeck et al. 2002). Markov chain Monte Carlo (MCMC) methods are used to approximate the posterior probabilities of trees and allow contemporary Bayesian methods to be computationally feasible

(Huelsenbeck et al. 2001, 2002). The MCMC method is used to sample the posterior probability distribution of trees. The application of the MCMC to phylogeny inference is summarized in Huelsenbeck et al. (2001, 2002) and Pagel et al. (2004). The general process of MCMC, which is used to approximate the posterior probability density, is as follows. First, a random tree is selected. Second, another tree is proposed by changing one variable of the original tree (e.g., topology, branch length, model parameters, etc.), and the two trees are compared using the Metropolis-Hastings algorithm (Metropolis et al. 1953; Hastings 1970; Huelsenbeck et al. 2002). If the tree represents an improvement, it is accepted or sampled. If not, the tree is either accepted or rejected proportional to the likelihood ratio between it and the previous tree (Pagel et al. 2004). The chain stabilizes after a sufficient period of run time (called the "burn-in"). Once stable, the chain randomly walks through the universe of trees, sampling each tree in proportion to its frequency in the actual posterior density (Pagel et al. 2004). The longer the chain is run, the greater precision with which the actual posterior distribution of trees is approximated (Pagel et al. 2004). Metropolis-coupled MCMC uses multiple, simultaneous Markov chains, improves mixing and convergence, and allows exceedingly large data sets that are beyond the scope of conventional single-chain MCMC Bayesian methods to be analyzed (Huelsenbeck et al. 2001, 2002).

Advantages of Bayesian Likelihood

A major advantage of the Bayesian method is the ease with which posterior probabilities can be interpreted (Huelsenbeck et al. 2002). Under the assumption that the evolutionary model is true and that the MCMC has accurately sampled the posterior probability distribution, the posterior probability value represents the probability that the tree is correct given the data and the priors. Similarly, the proportion of trees in the MCMC sample in which a monophyletic group appears represents the probability that the clade is "true," given the caveats of priors, model, and data.

As in maximum likelihood analyses, the result of the Bayesian analysis is dependent on the model of sequence evolution being "correct" (Kelchner and Thomas 2007). Bayesian approaches to phylogeny require a likelihood value of a given tree topology for their calculation of the posterior probability of that evolutionary scenario. The likelihood parameter in the Bayesian method uses the same models and their associated assumptions as the maximum likelihood methods described above, and the caveats inherent in maximum likelihood phylogeny estimation with respect to evolutionary models also apply to Bayesian analysis (see above discussion of likelihood criticisms).

Some view it as an advantage that Bayesian analysis requires the incorporation of previous knowledge or beliefs in terms of prior probabilities. The mechanics of formulating priors can be difficult if one chooses to base these on the results of previous analyses or taxonomy ("complex priors," Huelsenbeck et al. 2002). Making the prior probabilities of each tree equal eliminates the use of complex priors, as well as any a priori assumptions that any hypothesis is more probable than any other in light of prior beliefs; clearly this approach is not in the true Bayesian spirit.

Criticisms of Bayesian Likelihood

Bayesian approaches to phylogeny require a likelihood value of a given tree topology (i.e., phylogenetic hypothesis) for their calculation of the posterior probability of that evolutionary scenario. The likelihood used in the Bayesian method requires the same models and their associated assumptions as the maximum likelihood methods described above, and thus all of the cautions inherent in maximum likelihood phylogeny estimation also apply to Bayesian analysis (see above discussion of likelihood criticisms). Analogous to likelihood, the posterior probability of a tree involves summation over all possible trees, including all their possible permutations in terms of branch lengths and substitution-model parameters (Huelsenbeck et al. 2002). This is impossible to perform in most practical applications due to computational and time constraints and requires that posterior probabilities themselves must by necessity be approximated. Additionally, Bayesian methods require further assumptions about the prior probabilities associated with each tree. Making the prior probabilities of each tree equal minimizes any a priori assumptions that any topology is more probable than any other.

Harper (1979) had considerable foresight in devising a Bayesian framework aimed toward constructing and testing phylogenetic hypotheses, although this method was largely conceptual and significantly differs from the current practice of Bayesian inference in phylogeny. Likewise, Brooks et al. (1986) proposed the D-measure, based on the statistical entropy calculations in information theory. Tribus and McIrvine (1971) suggested that van der Waals proposed the first link of Bayesian reasoning to statistical concepts of entropy in 1911, when he suggested that the highest entropy state for a system was its a priori most probable state. Lewis (1930) subsequently suggested that increases in entropy were associated with losses of information, and Shannon (1948) used the statistical formulation of entropy as a synonym for expected uncertainty as a foundation of information theory. Kullbach (1951) reinforced the link between information theory and Bayesian reasoning by using the term surprisal (first introduced by R. Levine) as an indicator of departure from the most probable/most expected state. Brillouin (1962) showed that there was consistency between Shannon's use of entropy in information theory and the use of entropy in statistical mechanics and probability theory. Jaynes (1957a, b) derived the formal relationship underlying this consistency and proposed the first entropy maximization principle, in which the maximum entropy state of a system could be formally construed as the most probable state.

Gatlin (1975) added to this conceptual framework by discussing two forms of redundancy in the context of biological (specifically DNA sequence) evolution. R-redundancy results from the repeated occurrence of the same symbol in order to get a message across. This is one way to ensure proper communication of a message, but since each symbol must be repeated, R-redundancy is also associated with reduced message variety. D-redundancy, or Shannon redundancy, results when a single symbol appearing once always subsequently stands for the same thing. D-redundancy is associated with increased message variety, since no symbol need be repeated and thus a larger number of possible messages could be transmitted using the same number of symbols than for situations in which some symbols were repeated. This state may also be associated with reduced message fidelity, however, since missing the symbol initially results in a loss of information subsequently, without hope of a recurrence of the symbol. Gatlin associated D-redundancy with optimal coding in communication systems. Finally, R-redundancy is associated with low information density per symbol (each symbol represents only itself) and D-redundancy with high information density per symbol (each symbol represents many observations).

Brooks (1981) first showed that phylogenetic systematics operationally produced the lowest possible informational entropy configuration for a set of observations over a given set of taxa. This corresponds to the state of greatest difference between H_{max} and H_{obs}, or the configuration closest to H_{min} possible given the data. Brooks et al. (1986) later proposed an informal link between this and Gatlin's D-redundancy, proposing the so-called D-measure for choosing optimal phylogenetic trees on the basis of maximum information density.

Neither Brooks (1981) nor Brooks et al. (1986) related these discussions explicitly to Bayesian reasoning, but there is a clear connection. Following Jaynes (1957a, b), Bayesian approaches in information theory are thus those for which the a priori subjective hypothesis is determined by the entropy maximum principle – the a priori most probable result is the H_{max}, in direct analogy is with the maximum entropy state being the most probable for a closed system. This analogy works in a Bayesian framework if the set of observations used in any analysis is a closed subset of all possibilities, i.e., the estimate of H_{max} is based on a subjective subsample of an imperfectly known universe of characters, and no additional observations are introduced during the testing procedure.

The entropy maximum is not only analogous to the a priori expected *most probable* state; it is also the state of lowest *information density* of the observations, hence least informative, hence least surprising (in a Bayesian sense). For any set of observations (subjective in the sense that they are a subjectively selected subset of all observations, drawn from a universe for which the actual size or distribution of variables are unknown – even if the observations are obtained objectively), the most probable state (H_{max}) can be computed. (H_{min}) can be computed to the least probable state, which is the state of greatest information density for the observations and thus the state of greatest surprise.

The most powerful analysis of such data is one that seeks to find the most improbable/highest information density configuration permitted by all the data at hand. For phylogenetic analysis, H_{max} and H_{min} can be calculated from the basic data matrix (hence, H_{max} is a priori), whereas H_{obs} is calculated over a set of trees (hence, it is a posteriori). The preferred result is the one in which H_{obs} approaches H_{min} as closely as possible.

Applying the D-measure leads to a number of conclusions for phylogenetics analysis (Brooks et al. 1986): (1) information density is proportional to evolutionary conservatism; (2) dichotomous solutions are preferred over polytomies, as each instance of conservative evolution increases information density; (3) branching topology is irrelevant, and there is no a priori difference between symmetrical and asymmetrical tree structure in terms of information density, since it is the information that produces the tree, not the reverse; (4) for any data set, the most information-dense set of relationships of all taxa over all characters allowed by the data is the shortest tree; and (5) when there are multiple most parsimonious trees, ACCTRAN provides a more information-dense summary of the data than DELTRAN.

This version of Bayesian thought applied to phylogenetics, therefore, devolves to straightforward support for Hennigian methods. Missing from this formalism are statistical significance tests. There need to be two of them: first, is the result significantly different from the a priori expectation ($H_{\max}$), and second, are less information-dense alternatives (e.g., other equally parsimonious trees or less than most parsimonious trees) for the same set of data significantly different from each other?

How to Decide What Method(s) to Use

There are no objective means by which one can choose among these methods. Consequently, it is no surprise that some of the most contentious interactions among phylogeneticists concern the very subjective issue of which methods are best. It is common for groups of contending scientists, faced with such a situation, to resort to philosophical arguments in an attempt to claim priority for one viewpoint over another on the basis of some set of first principles. This has certainly been the case with phylogenetics.

Popper

The first salvo fired in this conflict was by Wiley (1975), who, in defending phylogenetic systematics against claims that it was not falsifiable, proposed that phylogenetic hypotheses of homology could be seen as an exercise in hypothetico-deductive reasoning.

> Once a hypothesis of homology is formulated from the world of experience, it is tested in two phases: by its own set of potential falsifiers and by a set of potential falsifiers of the phylogenetic hypothesis to which it belongs as a proper subset (i.e., it is tested by other hypotheses of synapomorphy through the testing of the phylogenetic hypotheses which they corroborate). Both phases of testing must be done under the rules of parsimony, not because nature is parsimonious, but because only parsimonious hypotheses can be defended by the investigator without resorting to authoritarianism or apriorism. (Wiley 1975, p. 236)

Hypotheses of homology, together with their connected hypothesis of phylogenetic relationships, can be tested by other independently proposed homologies, which then represent the so-called potential falsifying hypotheses (Popper 1968, p. 87). Wiley emphasized that such a process is not circular, but represents a case of "reciprocal illumination," something Hennig (1966) also claimed. Wiley noted that the preferred phylogenetic hypothesis is the one that has been refuted the least number of times. That Hennigian phylogenetics was justified by the hypothetico-deductive approach of Popper quickly gained support and still has strong adherents (Kluge 2003) who consider Hennigian phylogenetics to be strongly deductive in nature.

De Queiroz and Poe (2001) attempted to link Popperian thought with likelihood approaches, suggesting that likelihood is the basis for Popper's degree of corroboration. However, for Popper, corroboration was embedded in a falsificationist context, whereas these authors sought to decouple Popper's ideas about corroboration from those about falsificationism. In this context their degree of corroboration is identical with Popper's formalization of degree of confirmation (Popper 1997, p. 222). This merely leads back to the position that if a model is accepted as true or highly typical, its use is justified. But no objective means is provided for verifying or falsifying the validity of the model beyond the arguments about statistical consistency, which has shortcomings discussed below. Regardless of semantic arguments about corroboration and confirmation and possibly a high degree of revisionist interpretation of Popper's views on the relationship between corroboration and falsification, these arguments do not counter the basic observation that maximum likelihood methods are more inductive than deductive in nature. And, if the difference between the epistemological and the ontological parsimony approaches is the difference between a preference for deduction and a preference for induction, the history of science shows that there is no objective means for choosing between them.

However popular it has been among some systematists, this battle of philosophical perspectives has been subject to extensive criticism by philosophers, best summed up by Sober (1988), who identified phylogenetic analysis as abductive, that is, neither exactly deductive nor exactly inductive. This is explained by the fact that the phylogenetic inference is a retrodictive analysis of historically unique events. Among other things, this means that inference from effects to cause(s) is ampliative. Systematists only observe the effects under the causal theory of descent with modification (i.e., observable synapomorphies), but possible causes for conflicting data are also reversals and parallelisms. Thus, multiple conclusions about the cause(s) are possible in phylogenetic inference. By contrast, true deduction is nonampliative, enabling inferences from cause to effect(s), with singular conclusions for any given analysis.

Statistical Consistency

A method is said to be statistically consistent if it converges on the true tree as progressively more data are added to the analysis. One reason likelihood has gained popularity in the last two decades is that it has been suggested that other methods of phylogenetic inference, namely, Hennigian parsimony, are statistically inconsistent under certain, largely hypothetical models of evolution (Felsenstein 1978; Penny et al. 1992). The region of statistical inconsistency has been referred to as the "Felsenstein Zone," and it is the result of a process termed "long-branch attraction." The long-branch attraction problem occurs when convergent homoplastic changes are more frequent than nonreversed changes in an informative part of the tree (Felsenstein 1978). This confounds Hennigian phylogenetic systematics because, under the Auxiliary Principle, the convergent homoplasies will tend to be considered as homologies and thus the taxa with their convergent "long branches" will be grouped together (Hennig 1966; Felsenstein 1978). In simplest terms, when the *data are lying* about the relationships of the taxa, phylogenetic systematics (i.e., Hennig 1966) may fail to discover the true relationships. How often this occurs in nature is unknown, but Huelsenbeck (1997) has cited one case involving insects as exemplifying the long-branch attraction problem in a real data set (but see Siddall and Kluge 1997, pp. 319–320). The concern that "noise" or random data misdirects phylogenetic systematics is also overblown (Wenzel and Siddall 1999).

Maximum likelihood has been reported to exhibit the favorable property of statistical consistency in these situations (Felsenstein 1978; Penny et al. 1992; Yang 1994). It is true that in statistics the maximum likelihood estimate of a parameter is consistent (Fisher 1922; Edwards 1972). Simulation experiments have shown this to be true in phylogenetic context (Yang 1996), but *only* when the same random model used to generate the data is used and/or only when a certain correction factor is implemented (Steel et al. 1993; Siddall and Kluge 1997; Steel and Penny 2000; Goloboff 2003). It is an important caveat that maximum likelihood methods are only consistent (i.e., converge on the "true tree") under a certain set of circumstances which typically requires that the "correct" model is used but that the correct model and the true tree are both unknowable for real systems.

Farris (1973) suggested a protocol by which parsimony methods could be interpreted as derivatives of statistical estimation methods. This probabilistic view of parsimony was critiqued by Felsenstein (1973, 1978, 1981, 1983), who focused on the statistical deficits of parsimony when viewed as a likelihood method. In general, parsimony and likelihood approaches produce the same results under the assumption of particular parameters for parsimony, i.e., low rates of evolutionary changes or equal rates of evolution among the observed lineages or low rates of homoplasy (Felsenstein 1983). It has also been demonstrated that parsimony-based methods can be consistent (Steel et al. 1993; Siddall and Kluge 1997; Steel and Penny 2000, with a correction factor). Siddall and Kluge (1997) and Steel and Penny (2000) correctly point out that all methods are potentially consistent or inconsistent (Steel et al. 1993). Statistical consistency is not a property of a method, but the property of a specific data set, the model, and specific situations.

Likelihood methods generally require that the processes maintaining current systems were always present and consistent in the past, and this is likely not the case. Models range from relatively simple to complex, but all make approximations for computational efficiency that impair evolutionary realism. When the model is insufficient or inappropriate, as is common, arguments of statistical consistency are rendered moot. As noted earlier, frequency probability theory is violated in the calculus of current maximum likelihood methods (due to violation of independence requirements). Maximum likelihood uses a method intended to predict the future out of a range of simultaneously possible outcomes to infer a nonprobabilistic historical singularity, the evolutionary relationship of organisms.

It appears that neither epistemological nor ontological parsimony methods for inferring phylogenies can be justified, or given precedence over the other, by any part of Popper's philosophy. Nor can either approach be given priority by appeals to statistical consistency. And, finally, each approach can be given a Bayesian interpretation. Is there an objective way to choose between or to reconcile these subjectively divergent approaches?

An appeal to collegial pluralism seems like a good idea at first glance. It is becoming a common practice for an author to present maximum parsimony, maximum likelihood, and Bayesian analyses of the same data set. There is increasing evidence that in many cases both parsimony- and likelihood-based approaches reach the same topology (Rindal and Brower 2011). In a study of 1,000 papers published between 2007 and 2009 in the journal *Molecular Phylogenetics and Evolution*, Rindal and Brower (2011) found that there was strong incongruence between the results of parsimony and likelihood analyses in only 2 out of 504 studies that used multiple methods; in 502 of 504 studies, maximum parsimony and likelihood approaches yielded the same results. Similarly, Wiley and Lieberman (2011) showed that Bayesian and parsimony analysis of the same data produced the same results. Although the "true" evolutionary history of a clade is unknowable, these results suggest that with the inclusion of sufficient data (morphological characters or genetic sequences), different phylogenetic methods converge on the same results. Rindal and Brower (2011) "encourage the use of analytical approaches unencumbered by ad hoc assumptions that sap the explanatory power of the evidence."

Individual data analyses without reference to an explicit evolutionary model or hypothesis (i.e., epistemological parsimony) are not explanations. They are descriptions, admittedly highly sophisticated descriptions, but just that. Fitting data to a model provides explanations, but does not give any means of testing the veracity of the model or its assumptions. Independent description and assessment relative to explanatory models both appear to be necessary but not sufficient for robust explanations. Or, if models do not agree with the empirical data, chances are the models, not the data, should be reevaluated. This is not an antimodel stance. A mutually reinforcing and mutually modifying dialogue between models and empirical discovery enhances progress.

Kluge (1991, 1997, 1999) has argued persuasively that historical sciences progress through cycles of discovery and evaluation, both of which are necessary but neither of which is sufficient for complete understanding and both of which require objective methods of study. Hennigian (epistemological parsimony) analysis is the best discovery method in phylogenetics. This is because its results are dependent on a minimum of a priori assumptions, and thus the range of potential discoveries indicated by the data is greater than for any ontological parsimony approach. At the same time, this feature of Hennigian phylogenetics renders it relatively weak as an instrument of evaluation.

It appears that the various maximum likelihood and Bayesian likelihood approaches are admirably suited as evaluation methods. Epistemological and ontological parsimony methods can be used together in a form of reciprocal illumination, not in the narrow sense of deriving a tree from multiple characters, but in a broader sense of cycles of discovery and evaluation. How would this work?

To begin with, suppose a Hennigian analysis, a maximum likelihood analysis, and a Bayesian analysis produce the same result. This suggests that a relatively independent discovery (the Hennigian tree) supports an evolutionary model (the likelihood tree). In this case, no one should have any concerns using the likelihood model to infer divergence rates on the Hennigian tree. Now, what does it mean if these different analyses do not produce the same result? The findings by Rokas et al. (2003) suggest that all such situations are an indication that not enough data have been used. Their total-genome (107 gene sequences) analysis of a clade of 7 yeast species showed that a minimum of 20 genes (i.e., roughly 20 % of the genic characters possible) was required to ensure that all methods produced the same phylogenetic tree. Different methods gave different results when not enough characters were used to compensate for ambiguities of various kinds in the data, which are handled in different ways by the different methods discussed in this chapter. These results were anticipated experimentally by Hillis et al. (1992, 1993; Huelsenbeck and Hillis 1993), who produced a phylogeny for bacteriophages maintained in the laboratory. They discovered that most model-based approaches and Hennigian phylogenetics converged on the same and true (since it was known) phylogeny as more and more traits were sampled. These results would seem to suggest that the primary response to any situation in which the different approaches to phylogenetics produce different answers should be

> . . . When in doubt, get more data. (Brooks and McLennan (2002, p. 148))

What should systematists do while waiting for enough data to give the same answer with all methods? Hillis et al. (1992, 1993; Huelsenbeck and Hillis 1993) showed that when a limited quantity of data is available, some models generate the correct phylogeny better than Hennigian approaches. Although this finding has been interpreted by some as an indication that model-based methods are inherently superior to Hennigian methods, Hillis et al. (1994) pointed out a significant tradeoff. Model-based approaches provide a distinct answer based on little data, but the confidence in that answer is proportional to the modeler's belief that the model used accurately reflects the evolutionary process over extended periods of time for the clade analyzed.

The issue becomes: Which model typically gives the truth? Hillis et al. (1992) took a critical first step by generating an experimental phylogeny. The next step is to ask, how typical of evolution is that phylogeny? Remember that the phylogeny (1) involved bacteriophages and (2) was generated in the laboratory according to rules invoked by the researchers. Some have suggested that prokaryote evolution has produced not a phylogenetic tree but a highly reticulated network, in which case the experimental phylogeny produced by Hillis et al. (1992) is not typical of evolutionary history for their model organisms. Nonetheless, their results may still be typical of phylogenesis for eukaryotes.

More important is the question, how large a role has the historical contingency that is such a critical part of Darwinian mechanisms played in phylogenesis? Some have asserted that such contingencies do not affect phylogenetic reconstruction, while others have asserted the opposite (see Yang and Bielawski 2000 for a review). Seen in this light, it is possible that the reason Hennigian and model-based approaches converge with increasing data is that the more data considered, the more historical contingencies will play a role, in which case model-based approaches will progressively choose models whose set of "allowed possibilities" most closely approximates the minimal "a priori restrictions" of Hennigian phylogenetics. For example, Gissi et al. (2000) reported lineage-specific evolutionary rates for different mammalian mtDNA genes, suggesting that recovering the correct phylogeny might require a different mode for each gene, and used their findings to support contentions by other molecular systematists that, given uncertainty about the true phylogeny, the model that will give the correct phylogeny is not known and thus as many genes as possible is analyzed to help determine the appropriate model (Mitchell et al. 2000). For those researchers, the appropriate response to the assertion that "Nature is not as simple as our models . . .. But this should not be taken as a criticism of the use of a model" (Pagel 1992) is "Yes, it should" (Wenzel and Carpenter 1994).

This is the conundrum facing systematists. The next step involves a form of reciprocal illumination. That is, use the Hennigian result, rather than ModelTest, to determine the best likelihood model (i.e., what likelihood model gives the Hennigian tree). Then use the implied divergence rates from that model to add an explanatory context to the phylogenetic description without fear of introducing an element of circularity (by using the same model to build the tree and to test using the tree). When repeated across a variety of clades, this approach might suggest that some models fit the data more often than others, thus shedding light on the *general* process of evolutionary divergence patterns and rates. Perhaps some models would be suitable so rarely that they could be excluded from consideration of such general processes.

Similarly, one could use the maximum likelihood model "chosen" by the Hennigian analysis to assess the accuracy of the phylogenetic reconstruction, e.g., by linking the inferred divergence times with biogeographic or stratigraphic data. A likelihood framework has been used to incorporate or evaluate the probability of the phylogenetic hypothesis given the stratigraphic (i.e., temporal) distribution of taxa in the fossil record (Huelsenbeck and Rannala 1997b; Wagner 1998). These analyses require additional assumptions about the completeness of the fossil record and the reliability of the stratigraphic correlations. Wagner (1998) presented an analysis of hyaenids in which the strato-likelihood tree was ten steps longer than the most parsimonious tree, but it was putatively more consistent with the fossil record of the taxa. If the phylogenetic tree corresponds to a model that is in stark contrast with fossil evidence, it is time to get more data and reassess your tree and also time to dig for more fossils.

Phylogenetics in Paleoanthropology

This is an exciting time for paleoanthropologists to be involved in evolutionary biology. New discoveries of previously unknown primates and new fossil material of poorly known taxa are constantly changing perspectives on how close human relatives evolved and behaved. Phylogenetic systematics is a powerful investigative tool for generating and evaluating new evolutionary hypotheses. Its power lies in its transparency and paucity of assumptions; rather than appealing to the authority of what is "already known," phylogenetic analysis generates hypotheses that allow the raw data to speak for themselves. Phylogenetic systematics has been extensively employed in many branches of evolutionary biology and has stimulated new research directions and breakthroughs in the understanding of evolutionary patterns; however, it has yet to gain widespread use in paleoanthropology (Nunn 2011). Many workers use an intuitive approach to generate hypotheses of evolutionary relationships, combining chronological, geographical, and selected morphological data to produce their preferred pattern of relationships (Strait 2013). However, phylogeny-based methods allow the generation and testing of novel evolutionary hypotheses in ways that would not be possible without objective phylogenetic data. Although not as widespread in paleoanthropology as in other disciplines, a large and growing number of paleoanthropologists use phylogenetic systematic methods in evolutionary studies of the primates (e.g., Groves 1978; Strasser and Delson 1987; Begun et al. 1997; Nunn 2011; Strait 2013; Strait et al., chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3").

Currently, the areas of most vigorous debate and prolific research in the application of phylogenetic techniques to the primate fossil record concern the following: (1) issues of morphological character choice, (2) whether human evolution is best interpreted as an evolving lineage of many grades (primarily through anagenesis) or as a series of speciation events with many extinct branches (primarily through cladogenesis), (3) the incorporation of landmark-based geometric morphometric characters in phylogenetic analysis, and (4) the use of ancient DNA in phylogenetic analyses of recent human lineages.

How to Choose Morphological Characters

The choice of which characters to include is one of the first steps in a phylogenetic analysis and also one of the most critical. The features chosen, how they are coded, and their polarity (whether they are determined to be primitive or derived) are what determines the final tree topology. As such, the procedure for choosing and describing characters is the subject of vigorous and necessary debate in all primate systematics, but perhaps most passionately by those in the field of human phylogenetics.

Some paleoanthropologists are skeptical about the utility of morphological characters for understanding evolutionary relationships; they suggest that many characters are the result of convergent evolution and thus not informative about evolutionary relationships. Some have suggested that complicating factors *specific* to hominins may result in incorrect results using phylogenetic systematics (e.g., Lieberman 1999; Collard and Wood 2000, 2001, 2007; Hawks 2004). Hawks (2004) explored the degree to which cladistic methodology is able to clarify relationships within hominins. He cited problems with character choice, character independence, atomizing continuous traits, and coding polymorphic characters as key causes undermining the reliability of phylogenetic methodology. Collard and Wood (2007) suggest that in hominins the ratio of homoplasies to homologies is about 1:2, which results in multiple most parsimonious trees. Homoplasies may be the result of convergent evolution, including tightly connected morphological constraints termed "integrated cranial modules" (Goswami 2006; Cardini and Elton 2008; Goswami and Polly 2010; Gómez Robles and Polly 2012); or they may be phylogenetically misleading morphological similarities due to nongenetic factors related to mechanical loading (termed "homoiologies") (Collard and Wood 2000, 2001, 2007). Homoiologies have been suggested to be especially prevalent in primates compared to other groups (Collard and Wood 2000, 2001, 2007; Grehan and Schwartz 2009). These concerns about character choice are based on the idea that a set of characters have all evolved in concert, as a result of convergent selection vectors, yet could produce a robust Hennigian result that was nevertheless an incorrect depiction of phylogeny.

Strait and Grine (2004) found that when they included extinct taxa, craniodental characters produced a result that is consistent with the hominoid phylogeny based on molecular data. Based on quantitative characters (cranial and dental measurements) in extant hominoids and papionins, Collard and Wood (2000, 2001) found that correlated functional convergences in the catarrhine face and jaws made phylogenetic analyses using only those characters unreliable. However, in 2007, Collard and Wood reported that phenotypically plastic features of the hominoid face were actually congruent with the molecular phylogeny. Similarly, von Cramon-Taubadel (2009) and von Cramon-Taubadel and Smith (2012) found that measurements of the cranium and mandible reflected genetic relationships in hominoids, particularly when humans were removed. In a total evidence analysis (including both morphological and molecular data), Lehtonen et al. (2010, 2012) used a total evidence approach to refute the hypothesis that humans and orangutans are sister taxa (Grehan and Schwartz 2009). The total evidence approach is becoming more common; most systematists are realizing that incorporating as much data as possible often results in a more robust hypothesis consistent with multiple lines of evidence (e.g., O'Leary and Gatesy 2008; Wiens 2009; Wiens et al. 2010).

Integrated functional complexes potentially exist in many other taxa; for example, Goswami (2006) found that diet was correlated to morphological similarity in some carnivorans. However, Goswami and Polly (2010) found that in primates, trait correlation did not have a strong influence on morphological evolution over long time periods. It is true that for any data set in which correlated homoplasies outnumber homologies, Hennigian methods will produce an incorrect result. Which characters are homoplasious is not known a priori, so correlated homoplasies cannot be known a priori. However, if there are empirical data showing that characters are non-independent, the solution is to change the way in which characters are coded.

Coding integrated cranial features as separate discrete characters would violate Kluge's Auxiliary Principle (Brooks and McLennan 2002), which assumes characters are independent. In this way, the accumulation of developmental and functional data informs character choice based on empirical evidence rather than subjective supposition. Overall, if characters are known to be correlated, they should not be treated as independent in a phylogenetic analysis. However, in the absence of evidence of non-independence, the default treatment of all characters is to initially score them as independent and critically assess the results.

These examples illustrate how methodological choices, like which taxa and characters to include in an analysis and the level at which an analysis is conducted (intergeneric, interspecific, or intraspecific), can have dramatic effects on the results. However, because these choices are explicit, the results are open to reanalysis and interpretation by other researchers, which enables the procedure to be refined and permits a continuous expansion of data sets. Through incorporation of testable phylogenetic techniques and in reference to specific, falsifiable phylogenetic hypotheses of relationships, researchers are able to converge on a consensus.

Speciation Mode: Anagenesis Versus Cladogenesis in Hominins

One of the critiques of applying phylogenetic methods to the hominin record has been that the method forces each taxon onto a terminal branch; the default mode of speciation in the end result of a phylogenetic analysis is cladogenesis. However, phylogenetic systematics does not negate the possibility of anagenesis; in fact, it allows an explicit test of that hypothesis. A species can only be ancestral to another if it is reconstructed as the sister species and lacks autapomorphies. Although the final tree may place a possible ancestor on a neighboring branch, through critical evaluation of the results, the hypothesis can be assessed that an extinct species is a candidate for a direct ancestor. Therefore, phylogenetic systematics does not ignore the possibility of anagenesis; it simply requires post hoc evaluation. For hominin systematics, when there is a real possibility of ancestor–descendant relationships among the taxa of interest, this hypothesis can be tested by using both the pattern of relationships and reconstructions of character evolution. For example, Kimbel et al. (2006) performed a phylogenetic analysis using operational taxonomic units (OTUs) based on geographical location to test the hypothesis that *Australopithecus anamensis* was the direct ancestor of *A. afarensis*. Their results supported this hypothesis, because the two species are chronologically separated and *A. anamensis* has no apomorphies that are not also present in *A. afarensis*. Likewise, Antón (2003) proposed that *Homo erectus* was a widespread, variable, long-lived species composed of "geographically replacing allotaxa." These fascinating hypotheses can be tested using a comprehensive phylogenetic framework, which would also allow ancestral character states to be reconstructed and morphological evolution assessed within the clade.

Interestingly, there is much less debate about non-hominin primate phylogeny reconstruction, for example, in early primates (Rose et al. 2011) and papionins (Gilbert 2011). This may be due to the taxonomic level of the analysis; it may be easier to reconstruct relationships among species that are more distantly related to each other. It also likely reflects the extreme interest in hominin taxa as opposed to other groups of organisms.

Geometric Morphometric Methods in Phylogenetics

The popularity of geometric morphometrics (GM) has exploded in paleoanthropology in recent years (Slice 2005, 2007); geometric morphometrics is a collection of methods that analyze biological shape using landmark coordinates, allowing the user to conduct powerful multivariate statistical analyses (Slice 2007). These techniques can be applied to a number of research areas including functional morphology, allometry, development, inter- and intraspecific variation, as well as phylogenetics. In some studies, GM data are directly incorporated into a phylogenetic analysis during the character coding phase. For example, Cardini and Elton (2008) applied 3D morphometrics to assess how concordant the phylogenetic signal from different cranial regions was with a molecular estimate of phylogeny in guenons. They found that only the shape of the chondrocranium had a phylogenetic strong signal. Gilbert (2011) used 3D morphometrics to extract phylogenetically informative characters from the papionin basicranium. He was able to eliminate the effects of allometry on cranial shape and generate cranial characters to incorporate into a phylogenetic analysis. Von Cramon-Taubadel and Smith (2012) used GM to test whether different regions of the hominoid cranium were reliable indicators of phylogenetic relationships. They found that all regions of the hominoid cranium were strongly congruent with molecular estimates of phylogeny.

In other studies, the shape of a morphological feature is mapped onto a previously constructed phylogeny – one that was constructed excluding those shape characters (e.g., Wiley et al. 2005; Fleagle et al. 2010). The results of shape change over time are then interpreted based on the evolutionary pattern suggested by the tree topology. This allows researchers to address many different questions and estimate the predicted ancestral morphology at a node (Wiley et al. 2005; Nunn 2011). For example, Wiley et al. (2005) were able to estimate the skull shape of the hypothetical ancestors of old-world monkeys by combining information from molecular phylogenetic trees with three-dimensional surface scans of crania from extant species.

Increases in computational power and memory capacity, as well as innovations in statistical programs, have contributed to the advancements in the field, with many more likely to come. Paleoanthropology has been at the forefront of these developments, and there is likely to be an increase in the incorporation of GM data in phylogenetic analysis.

DNA Analysis of Recent Human Lineages

Paleoanthropology has also been on the cutting edge of sequencing ancient DNA, and many methodological improvements and startling discoveries have come from the extraction and amplification of badly degraded and extremely old DNA (e.g., Green et al. 2006, 2010; Krause et al. 2010; Reich et al. 2010, 2011; Meyer et al. 2012). These sequence data can be characters in phylogenetic analyses, and they also reveal evidence of interbreeding and the presence of unknown ancient lineages. See Hummel (chapter "▶ Ancient DNA," Vol. 1) for a detailed discussion. These new discoveries have the potential to generate further novel data, for example, integrating morphological characters with molecular characters in a "total evidence analysis" of hominins, including Denisovans and Neanderthals.

Conclusion

Phylogenetic analysis of any kind is merely an analytical tool. If the results of a Hennigian analysis are unexpected, there is nothing in the methodology that requires belief that the results of any given analysis are true. Rather, there are several possibilities: (1) the data are lying and no amount of additional data will rectify the problem, (2) the method is flawed, or (3) there are not enough data. If the first two possibilities are accepted, the systematist must choose a model that better fits his or her beliefs, experience, or understanding of the evolutionary process than do the data, then reconcile the data to the model.

If it seems likely that there are insufficient data, character choice needs to be exhaustive and explicit, new data should be included, hypotheses should be frequently reevaluated, and independent data should be used to corroborate or refute those hypotheses. Phylogeneticists must be explicit about the methods they use to generate and evaluate trees, and those evaluating their publications need to be aware and informed of the methods used. A list of character descriptions as well as the data matrix used to generate the tree should be available so that other researchers can evaluate the authors' character codes. Consistency indices, decay analyses, bootstrap values, branch lengths, and consensus trees are important procedures for assessing the robustness of results and should be published. As well, the techniques employed to generate these results should be clear. Other elements to consider when generating or evaluating phylogenetic hypotheses include: Do independent data (e.g., fossil dates, biogeography, behavior) corroborate or refute the hypothesis? Were all known taxa included? If not, is it because of poor preservation or lack of adequate sample size?

This transparency will facilitate discussion and evaluation of morphological characters and allow the generation and testing of novel evolutionary hypotheses. It will enable assessment of whether characters are functionally correlated, and result in the reevaluation of character choice and coding, strengthening the phylogenetic hypotheses generated. While the goal of a phylogenetic analysis is to reconstruct relationships based on shared, derived characters, the really interesting evolutionary enigmas in any clade are the homoplasies. These convergences and parallelisms direct attention to possible functional or environmental selection responsible for the visible pattern of evolutionary change:

> "Or, [there are] . . . four guiding principles: (1) phylogenetic trees are necessary but rarely sufficient for explaining evolutionary origins and diversification; (2) the systematist must always be responsible for well-formulated questions; (3) the systematist must always be responsible for the quality of the data used in any level of analyses, from generating phylogenetic hypotheses to testing general theories; and (4) everything learned implies yet more cycles of discovery and evaluation . . .". (Brooks and McLennan (2002: 22))

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Genetics and Paleoanthropology
- ▶ Molecular Evidence on Primate Origins and Evolution
- ▶ Patterns of Diversification and Extinction
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Population Biology and Population Genetics of Pleistocene Hominins
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology

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Homology: A Philosophical and Biological Perspective

Olivier Rieppel

Contents

Abstract

Current discussions of the concept of homology center on metaphysical and epistemological issues: what are homologs, and how can they be discovered? Homology is the relation of common ancestry shared by homologs. Homologs are the "same" parts of two or more organisms under every variation of form or function that are shared due to inheritance from a common ancestor. Homology is the key to phylogeny reconstruction, because the hierarchy of homologs/homologies is isomorphic with the phylogenetic hierarchy of taxa. Consequently, the discussion of homologs as evolving entities shares many parallels with the discussion of species evolution. Homologs are conceptualized as tokens of natural kinds that engage in causal processes of ontogeny, phylogeny, and physiology. Operational criteria for the discovery of homology are the topological relations (connectivity) shared by homologs. These operational criteria are (at least to some degree) grounded in ontogeny, where developmental modules may share the relation of homology. In that sense, the operational criteria for the

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O. Rieppel (✉)
Department of Geology, The Field Museum, Chicago, IL, USA
e-mail: orieppel@fieldmuseum.org; rieppel@fieldmuseum.org

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discovery of homology are aligned with the structure of the causal processes in which the homologs qua tokens of natural kinds engage. The discussion of concepts of partial homology and the complementarity of static (taxic, hierarchical) versus dynamic (developmental, transformational) approaches to homology reveals empirical as well as a semantic components.

Introduction

The pretheoretical use of the concept of homology reaches far back into the preevolutionary history of comparative biology (Panchen 1994). Belon (1555) is usually taken as *locus classicus* for the earliest illustration of the relation of homology (Fig. 1), although the concept must have been implicit in Aristotle's recognition of dolphins as mammals (Russell 1982, p. 6).

For Etienne Geoffroy St. Hilaire, the unity of type was based on the relation of "analogie," a concept that captured the correspondence of relative topological relations (*connectivité*) of constituent elements of the organism tied together

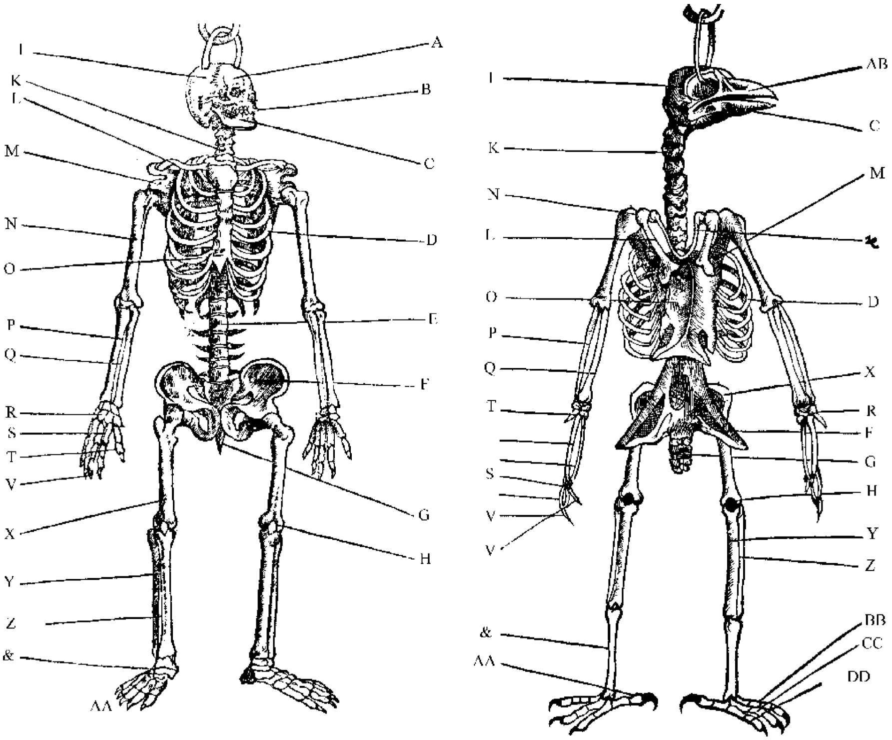

Fig. 1 In a comparison of the skeleton of man and a bird, Belon (1555) recognized the topological equivalence of constitutive elements (Courtesy of the Field Museum Library, Mary W. Runnells Rare Book Room)

throughout ontogeny by the blood-vascular system (Rieppel 1988, 2001). Geoffroy's "analogie" became Richard Owen's "homology," meaning "the same organ in different animals under every variety of form and function" (Panchen 1994, p. 40; Williams 2004, p. 192). Owen contrasted this concept with "analogy," meaning "a part or organ in one animal which has the same function as another part or organ in a different animal" (Panchen 1994, p. 40; Williams 2004, p. 192). Panchen (1994, p. 44) drew attention to the fact that, as used by Owen, homology and analogy were not necessarily mutually exclusive concepts, so a third term was required to characterize structures analogous between two or more organisms but not homologous. This was Lankester's (1870) "homoplasy." In fact, Lankester (1870) restricted the use of the term homology to its preevolutionary connotations; he called the evolutionary use of the concept that implies common ancestry "homogeny."

At the hands of Geoffroy St. Hilaire or Owen, homology was meant to capture structural correspondence, rooted in "laws of structure" as expressed during ontogeny. The relation of homology (and analogy) was reconceptualized (Kitcher 1993, p. 32) by Darwin (1859), who found that, on his theory, "unity of type is explained by unity of descent" (Darwin 1859, p. 206). The term homology continued to apply to the same constituent parts of organisms that were recognized as homologs by Owen, but the meaning of the term changed to something roughly like "shared similarity due to common ancestry." The history of the concept of homology has been variously sketched, sometimes in great detail (Panchen 1994; Williams 2004), and needs not to be retraced here. Instead, the focus of this chapter will be on issues that are central to the contemporary discussion of the concept of homology in systematics and developmental biology. How does "similarity" relate to the concept of homology, or, in other words, how can the relation of homology be rendered empirically accessible? Is there such a thing as "partial homology"? What does it mean to say, in Owen's words, that homologs are "namesakes," i.e., parts that "merit the same name" (Patterson 1988, p. 605), or that "the same names can be given to the homologous bones in widely different animals" (Darwin 1859, p. 434)? What does "sameness," "structural identity" (Wagner 1994), or "historical identity" (Grant and Kluge 2004) mean in reference to homologs, or, in other words, what kind of names refer to homologs? Are homologs particulars (individuals), denoted by proper names, or tokens of natural kinds, denoted by general names?

Semantics of Homology Statements

To better understand the semantics of homology statements, it is worthwhile to first introduce some distinctions, derived from Lankester's (1870) terminology (Table 1).

Homology assessment has been recognized to be, minimally, a two-step procedure (Jardine 1969; Rieppel 1988, 2004a; dePinna 1991; see Brower and Schawaroch 1996 for a more elaborate account). An initial conjecture of homology, based on some similarity relations that obtain between the organisms under

Table 1 A comparison of Lankester's (1870) and contemporary use of the terms homology and homoplasy (for further discussion, see text)

	Topology/connectivity	Congruence	Incongruence
Lankester 1870	Homology	Homogeny	Homoplasy
Contemporary systematics	Primary homology	Secondary homology	Homoplasy

analysis, represents an observational statement. The relation expressed by that statement was called homology by Lankester (1870), which corresponds to the "topographic homology" of Jardine (1969, p. 357) or the "primary homology" of dePinna (1991). Statements of primary homology are observational statements that relate to the organisms under analysis (Rieppel 2004a). The putative phylogenetic information content of those observation statements is subsequently tested on the basis of congruence (see further discussion later). If the statements pass the test (if they turn out coherent/congruent), they are called homology statements that correspond to dePinna's (1991) "secondary homology" (phylogenetic homology sensu Jardine 1969). These statements of (secondary) homology imply "similarity due to common ancestry" and therefore are theoretical statements, i.e., theoretical (meta) statements *about* the observational (object) statements (Rieppel 2004a). If coherence/congruence fails to obtain, the observation statements are said to be statements of homoplasy, which imply convergent similarity relations or chance similarity. Parallel evolution is said to result in a similarity relation between related lineages that is not inherited from their common ancestor. Consequently, congruence of observation statements (of primary homology) may theoretically be due to parallel evolution, but given the tools of phylogenetic systematics, there is no way to empirically distinguish (secondary) homology from parallelisms. From these considerations, Farris (1983) drew the agnostic (Sober 1985) conclusion that whereas incongruence undermines, congruence does not necessarily confirm phylogenetic hypotheses.

Observation statements deploy predicates that are meant to apply to the objects observed. For example, a chordate is an animal with a notochord; a "renate" is an animal with kidneys. The sentence "a chordate is an animal with a notochord" is of a subject-predicate structure, symbolized as Fx, where F is the predicate "… is an animal with a notochord" and x is the subject that is an animal with a notochord. More generally, "chordates" is the set of all animals that have a notochord, and renates is the set of all animals that have kidneys. The fact that homology statements deploy predicates (Mahner and Bunge 1997; Wiesemüller et al. 2003) threatens to create an ontological inconsistency in an evolutionary context that is rooted in what philosophers call the "one-over-many" problem: "the selfsame property [e.g., to have a notochord] can be instantiated by numerically different things [e.g., rabbits and tigers]" (Swoyer 2000, p. 2). The extension of a predicate is typically taken to be the set of all things to which the predicate truthfully applies: the extension of the predicate "… with kidneys" is the set of all animals with kidneys. But sets are abstract entities, not historical entities, and the semantic value of a predicate is usually taken to be a universal, not a particular (but see Swoyer 2000 for further discussion). Homology statements predicate properties of organisms, and properties, in contrast to particulars (individuals such as objects or bodies), are universals (properties include the attributes or qualities or features or characteristics of things) (Swoyer 2000, p. 2). Under the paradigm of nominalism, only particulars can claim existence (i.e., the occupancy of a particular space-time region), universals such as properties cannot. If we think of each term as referring to (denoting, designating) a thing (object, body), then predicates would have to refer to entities, with the consequence that universals, such as "redness" (*x* is red) or "rabbit-hood" (*x* is a rabbit), acquire some sort of Platonic existence as abstract entities. To avoid this conclusion, Devitt and Sterelny (1999) proposed to conceptualize predicates not as referring expressions but instead as expressions that apply to particulars (which in turn occupy a particular space-time region). For what would be particulars "when stripped of their clothing of universals" (Devitt and Sterelny 1999, p. 278)? The predicate ". . . is red" can thus apply to this or that or yet another apple, and the predicate ". . . is a tiger" can apply to this or that or yet another individual organism.

If the predicate ". . . is red" is applied to "this apple" (to which I point), then this apple is said to instantiate the property redness, but redness does not exist as a spatiotemporally restricted entity. In contrast, kidneys exist as spatiotemporally restricted entities: they can be removed or replaced by surgery. So what is the difference between "this apple is red" and "this creature is an animal with kidneys"? One way to look at the issue (Haack 1998, p. 133) is to claim that the predicate ". . . is red" marks out the set of all red things and apples are (or can be) members of that set. Similarly, the predicate ". . . is an animal with kidneys" marks out the kind of all animals with kidneys, i.e., the renates. The set of red things that includes apples, cars, and billiard balls is unlikely to be tied together by a unifying causal process, but the renates, which (for the sake of the argument) are here equated with vertebrates, are tied together by unifying causal processes, namely, those of ontogeny and phylogeny. In other words, redness is not a property that is causally efficacious; the set of red things therefore is not a natural kind. In contrast, to have kidneys is a causally relevant property that is shared by all renates, and it is in virtue of engaging in these causal processes that renates form a natural kind, as do vertebrates and also apples – red, green, or yellow – but not red things.

Under such analysis, individual tigers become tokens of a natural kind, namely, parts of the sum of all tigers. "Tiger" thus becomes a name associated with a natural kind term, and the extension of that natural kind term (of the predicate ". . . is a tiger") is the sum of all tigers, i.e., the natural kind tiger that is marked out by a common evolutionary origin. In other words, the common evolutionary origin is the relevant property that marks out the natural kind tiger. Each individual tiger that shares the same evolutionary origin is therefore a token of its kind. Each individual vertebrate is a token of the natural kind "renate" or "chordate," if the relevant property that marks out the natural kind "renate" or "chordate" is commonality of evolutionary origin.

Natural kinds come in hierarchies (Platts 1997): the individual lemon is not only a token of its proper kind but also a token of the natural kind "citrus fruit," as well as a token of the natural kind “fruit.” The same is true for animals: the individual tiger is a token of tigers, of “mammals,” and of “vertebrates.” A lemon can be squeezed, a tiger captured, and a kidney removed or replaced. The sum of all kidneys constitutes a natural kind; its tokens are instantiated by all renates. “Notochord” is a natural kind term; the tokens of its kind are instantiated by all chordates. Renates and chordates constitute a natural kind, if they share a common evolutionary origin; particular kidneys and notochords (taken from rabbits or tigers) are tokens of natural kinds that share a common evolutionary origin if kidneys and notochords are homologs of vertebrates. If kidneys and notochords were homoplasies (e.g., homoplastic in rabbits and tigers), they would be tokens of nominal kinds (the corresponding terms nominal kind terms). The key to “natural kindness” is the fact that the tokens of the kind take part in causal processes and that their properties are causally efficacious (Sober 1981; Quine 1994; Shoemaker 2003).

Conceptualization of homology in terms of natural kind term semantics offers a key to why homology statements have to be tied to a conditional phrase (Bock 1974), given the fact that natural kinds, as well as homologies, come in hierarchies. Let us follow Quine (1964) into a foreign country where people speak a language that I do not understand. In that situation, a native points at a passing rabbit and utters “gavagai.” Seeing what the native points at and hearing her utterance does not tell me whether the native means “rabbit,” “rodent,” “mammal,” or “vertebrate”. In a similar sense, the statement that “bird wings and bat wings are homologous” remains underdetermined. Given that statement only, I cannot decide whether it is right or wrong relative to the background knowledge of the currently accepted theory of vertebrate phylogeny. But if the statement is “bird wings and bat wings are homologous as (*qua*) tetrapod limbs,” I know that the statement is right; if it is “bird wings and bat wings are homologous as (*qua*) wings,” I know it is false, given the background knowledge (see the discussion of the “*qua* problem” in Devitt and Sterelny 1999).

Homologs have been claimed to be individuals, or historical individuals, on ontological grounds (Grant and Kluge 2004). The reason is that only particulars, or individuals, can take part in causal processes such as descent with modification. Sets, or classes, cannot. If homology is a property, and properties are universals that mark out sets, or classes, then homologs cannot evolve. On the analysis described previously, causally efficacious properties mark out natural kinds. The common evolutionary origin marks out the natural kind tiger, but it is individual tigers, i.e., the particular tokens of the natural kind, that engage in causal processes such as descent with modification. If homologous, the sum of kidneys constitutes a natural kind, but again it is individual kidneys, i.e., the particular tokens of the natural kind, that engage in causal processes such as ontogeny. However, ontogeny, or descent with modification, requires plasticity if evolution is to occur. In order for this to be possible, an adequately weak notion of a natural kind must therefore be invoked such as the “homeostatic property cluster natural kind” proposed by Boyd (1991, 1999).

Common evolutionary origin can be the (essential: La Porte 2004) property that marks out biological natural kinds, like taxa or homologs, but tigers and their parts, such as their kidneys and their parts, such as kidney tubules, share other properties as well. For example, tigers share a genetic constitution, which they transmit – more or less reliably – to offspring as they engage in the causal process of reproduction. Kidneys engage in the causal process of excretion, a function that changed in some regards as renates evolved from water to land. Tokens of natural kinds which in virtue of their properties engage in developmental and physiological processes must be capable of plasticity if evolution is to occur. On the other hand, variation must not be so rampant as to disrupt ontogeny or physiological function. The clustering of properties in a variable and partially overlapping pattern that characterizes homeostatic property cluster natural kinds is believed to be affected by homeostatic mechanisms, which are themselves plastic and capable of variation and change (West-Eberhard 2003). "Because the clustering in the world that defines such a kind can be an ongoing process, the properties in the cluster can sometimes vary over time, and the kind's boundaries can be historically delimited if the clustering is historically delimited" (Keller et al. 2003, p. 105). With genealogy itself being a homeostatic mechanism of property cluster natural kinds (Boyd 1999), the latter can also be conceived of as historical kinds (Sterelny 1994, p. 11), a perspective that accommodates species as well as homologs.

Similarity, Homology, and Congruence

The relation of homology is a theoretical concept because it is based on common evolutionary descent. Since common evolutionary descent cannot be observed, it must be inferred from observation. Traditionally, biologists will take some sort of similarity relation to be indicative of common ancestry (Rieppel and Kearney 2002). Indeed, under the paradigm of evolution, homology is frequently defined as "similarity due to common descent" (West-Eberhard 2003, p. 485).

However, similarity is a highly loaded concept. Goodman (1972, p. 437) called similarity "a pretender, an imposter, a quack," whereas Hull (1999, p. 35) found it "unanalyzed, perhaps unanalyzable." "As philosophers have long recognized, similarity without theory is empty" (Sober 1984, p. 336; see also Ruse 1988, p. 60; Dupré 1993, p. 45). So "similarity" is taken to be a primitive concept that cannot be further defined, and yet it is hardly possible to "imagine a more familiar or fundamental notion than this, or a notion more ubiquitous in its application" (Quine 1994, p. 42).

In the face of these problems, contemporary systematics has experienced the revival of an outdated empiricism (Sneath and Sokal 1973) that was thought to have been put to rest long ago. It consists in a purely instrumental-algorithmic approach to homology in which the array of all phylogenetic hypotheses possible for *N* number of terminal taxa is used as an instrument to generate statements of putative homology. As argued by Härlin (1999, p. 497), "too much emphasis is put on particular characters" given the "logical priority of the tree over the characters." Similarity as a tool of systematics is declared bankrupt, and theory is eschewed on grounds of lack of positive knowledge. Critical character analysis is rejected as a "disturbing trend toward data selectivity" (O'Leary et al. 2003, p. 861) by proponents of the "total evidence approach," who cite Kluge (1997) in support of the notion that inclusion of all data, including all "published data," results in a stronger test of homology and phylogenetic relationships (O'Leary et al. 2003, p. 862). But to eschew theory in favor of an instrumentalist-algorithmic approach to character analysis does not mean to take an atheoretical stance, and as pointed out by Ruse (1988, p. 60):

> As soon as one starts breaking organisms into parts, one must bring in theory . . . Take two bears, one white and one brown. Do they differ in one feature, or does one take each hair separately . . . The point is whether someone who explicitly eschews . . . theory has the right to combine all the hairs into one feature.

Proponents of the "total evidence" approach (Kluge 1989) argue, "there is no one operation for determining character states in this system-it can be anything that leads to the testable hypothesis of synapomorphy" (Kluge 2003a, p. 356; emphasis added). Even more drastic yet more sophisticated is Griffith's (Griffiths 1999, p. 225; emphasis added) assertion that

> cladistic analysis can proceed from a list of arbitrary measurements by looking for congruence among the evolutionary trees produced by different measurements . . . thus 'bootstrapping' itself into a reliable character set.

Such a data set, "holding itself up by its bootstraps" Audi (2003, p. 187), has been called the result of "phenetic cladistics: elegant analyses with many sources of error" (Wägele 2004, p. 109). "We might just [as well] stop tugging at our bootstraps altogether" (Quine 2001, p. 457).

Contemporary systematists see homology assessment as a two-step procedure: the conjecture of homology (primary homology statements sensu dePinna 1991) and the test of those on the basis of congruence (yielding secondary homology statements sensu dePinna 1991). With a misguided appeal to Popper's philosophy of science (Kluge 2003b, 2004), the proponents of the phenetic approach to cladistics consider the contextual origin of primary homology statements (conjectures of synapomorphies in Kluge 2003a) irrelevant, *as long as* there is a method to test those statements. The test of choice is not Popperian, however, but built on congruence. The issue is not whether an observation statement is accepted as falsifying the theory from which its negation was deduced, as is the case in Popper's hypothetico-deductivism (Rieppel 2003a, 2004b). Instead, the issue is whether character statements cohere to a degree that seems sufficient for the (provisional) acceptance of a phylogenetic hypothesis.

Patterson (1982, p. 74) considered Wilson's (1965) consistency test for phylogenies "a more rigorous formulation of my congruence testing." The work done by the test of congruence is to maximize the consistency of all available data in marking out an encaptic (inclusive) hierarchy. In a "pattern cladist" approach, Patterson (1982) took characters to mark out sets and analyzed the consistency of their distribution in terms of mutual inclusion, mutual exclusion, or overlap of the sets the character statements define. The same logic underlies "Hennig argumentation" (Hennig 1966), ultimately based on the "inclusion/exclusion principle"

(Wiley et al. 1991, p. 45). Accordingly, the test of congruence is based on logic as it tests for coherence versus contradiction of character statements, but logic has a linguistic foundation (Soames 2003, p. 136). Coherence and contradiction are logical relations that obtain between sentences only and the propositions they express, not between organisms and their parts. Kidneys and notochords cannot cohere or contradict each other, only statements about kidneys or notochords can. The test of congruence therefore does not test for descriptive accuracy, causal relevance of character statements, or the like. It only tests for coherence (consistency relative to a hierarchy of sets within sets or, in the present analysis, kinds within kinds) of character statements. That is why phenetic cladistics is prone to many sources of error. If the contextual origin of conjectures of homology (primary statements of homology) were indeed irrelevant, and if the test of congruence were indeed sufficient for phylogeny reconstruction, there would be no theoretical basis on which to reject the purely operational "punch-card approach" (Sneath and Sokal 1973, Fig. 3.1) to the automatic scanning of characters. If congruence and nothing else is used in a test of character statements, then the support for a phylogenetic hypothesis derives exclusively from the mutual support of the coherent character statements, without consideration of how those character statements do or do not refer (apply) to the organisms under analysis. The individual character statements, and with them the phylogenetic hypothesis they putatively support, potentially remain hanging in the air. Haack (1998, p. 27) found such inference to fall victim to the "drunken sailor argument" that invokes the picture of two drunken sailors who believe they can mutually support each other by standing back to back when both stand on nothing.

Of course there can be no doubt that character congruence, i.e., the coherence of character statements relative to a hierarchy, is a necessary condition for phylogeny reconstruction. Incoherent talk about the world makes no sense, not in phylogenetics nor in any other domain of discourse. But the mere coherence of character statements is not also a sufficient condition for phylogeny reconstruction. If they are not to be left hanging in the air, character statements must somehow be grounded in the organisms under analysis, i.e., rooted in causal theories of inheritance, development, and/or function. Homologies are natural kinds only if their tokens (at least potentially) take part in causal processes. To thoroughly investigate the genetic, developmental, even functional background of each character used in phylogeny reconstruction is beyond practical reach, however. Homology is a theoretical relation that has to be inferred from observation, but observation cannot proceed meaningfully without theory and outside the context of background knowledge (Hanson 1961; Haack 1998). Quite simply put: to be relevant to a theory, the predicate deployed by an observation statement must have a theoretical counterpart in the theory (a set of theoretical sentences) to which the observation statement is meant to relate to (Körner 1970; Mahner and Bunge 1997). Theory and background knowledge will therefore have to be brought to bear on observations that result in the formulation of primary homology statements. Even if the distinction is unsharp and sometimes difficult to draw, this is how relevant evidence is generally distinguished from total evidence (Haack 1998). More specifically, a method is required that will allow to ground primary homology statements at least approximately and certainly defeasibly (the hypothesis of primary homology may be wrong) in causal theories of inheritance and development. This method consists in the application of the "operational criteria of homology," such as topology and connectivity (Remane 1952; Riedl 1977 showed that the additional operational criteria of homology formulated by Remane 1952 ultimately all reduce to topology and connectivity).

Quine (1994, p. 43; emphasis added) found that "there is something *logically* repugnant about" similarity in its primitive, innate, unanalyzed, and unanalyzable sense (Goodman 1972; Hull 1999). But science sheds this kind of similarity as it matures. Quine (1994, p. 53) used chemistry as an example of a maturing branch of science, in which "comparative similarity of the sort that matters for chemistry can be stated . . . in terms of chemical composition. Molecules will be said to *match* if they contain atoms of the same elements in the same topological combinations." The causal efficacy of chemical kinds is thus explained as a consequence of the topological relationships of their constituent elements. This is exactly the kind of similarity that also matters for the relation of homology. Systematists do not look for any kind of similarity, but for a special kind that is established on the basis of operational criteria of homology, i.e., the relative topological position and connectivity of constituent parts of an organism (both morphological and molecular) in their temporal (ontogenetic) and spatial (ontogenetic, molecular) manifestations. Topology and connectivity yield the special kind of similarity that delivers promissory notes for potential homology. Sameness or (historical) "identity" has been invoked for homologs that carry the same name, but there is no "perceptual sameness" (Kluge 2003b, p. 236, and n. 12) in a comparison of the lower jaw of a shark and the outermost ear ossicle of a mammal. However, there is perceptional topological correspondence (during early ontogenetic stages) that justifies the conjecture of homology (Reichert 1837).

The operational criteria of homology can be compared to "correspondence rules" (Rieppel 2003b) which, stripped of their positivist background, mean nothing more than either an experimental setup or an observational procedure (Nagel 1961). Mahner and Bunge (1997) use the broadly equivalent term "indicator hypothesis" which, in the present context, would be hypotheses that do not tell us what homology is, but instead guide us how to "look for" potential homology. The operational criteria of homology have empirically been found to be eminently successful in the reconstruction of the tree of life (Remane 1952; Riedl 1977), which is why it may be assumed that they provide a (defeasible, i.e., potentially mistaken) proxy for the causal grounding of hypotheses of homology in theories of inheritance, development, and evolution. In Boyd's (1991, 1999) terms, the use of the operational criteria of homology seems to be well aligned with the causal structure of the world, at least to some degree, and defeasibly so (Rieppel and Kearney 2002). The use of operational criteria of homology cannot, therefore, be theory free. They do not establish a purely "operational" link that maps a theoretical statement of homology onto an observational statement of topological correspondence of parts. The theoretical background that justifies the use of operational criteria of homology is the recognition that topology and connectivity are expressed in development and that evolutionary transformation of morphology occurs through the transformation of development (see further discussion later). A similar adherence to correspondence rules is known in molecular systematics: "Alignment of sequences requires explicit and objective rules if inferences of positional homology are to be robust" (Hillis 1994, p. 349; but see Wheeler 1998).

Development and Homology

Homologs share a common evolutionary origin, but "neither traits nor representations of traits are transmitted to offspring. Instead, they are made-reconstructed-in development" (Oyama et al. 2001, p. 2). Both development and evolution can be conceived of as a "process of *construction* and *reconstruction* in which heterogeneous resources are contingently but more or less reliably reassembled for each life cycle" (Oyama et al. 2001, p. 1). Development results in pattern formation, an "activity by which embryonic cells form [spatially] ordered arrangements of differentiated tissues" (Gilbert 1988, p. 589), and comparative morphology analyzes these patterns in terms of topology and connectivity. Raff and Sly (2000, p. 102) noted that developmental modules "occupy specific physical sites within the embryo" and "exhibit varying degrees of connectivity to other modules within the embryo." This is the juncture at which the operational criteria of homology find their partial, and defeasible, causal grounding in the process of development. It is for these reasons that developmental modules, themselves natural kinds (Wagner 1996, 2001; Brandon 1999; Rieppel 2004c), have been identified as the "traditional units for claims about homology" (Winther 2001, p. 117). However, the use of ontogeny to causally ground homology statements is riddled with difficulties.

For Darwin (1859, p. 449), "... community in embryonic structure reveals community of descent. It will reveal this community of descent, however much the structure of the adult may have been modified and obscured." However, in the fourth edition of the *Origin* (1866 p. 312; see Peckham 1959), Darwin added: "... community in embryonic structure reveals community of descent; but dissimilarity in embryonic development does not prove discontinuity of descent." The reason is that structures considered homologs may share strikingly different developmental trajectories. A simple and classic example is the generally accepted homology of the vertebrate brain in spite of the fact that the neural plate delaminates, rather than invaginates, in teleosts. Hall (1995) presented a review of the role of ontogeny as a criterion of homology, concluding that "homology can no longer retain its historical links to shared embryonic development," for "there are so many examples of homologous structures arising from nonhomologous developmental processes" (Hall 1995, p. 8; see also Rieppel 1993; Hall 1994; Rieppel and Kearney 2002). But just as potential homologs can develop along different ontogenetic trajectories, so can a similar developmental background generate very distinct morphologies: "The transcription factors 'distal-less,' 'engrailed,' and 'orthodenticle' each have orthologs involved in patterning very different structural features in different metazoan taxa" (Mindell and Meyer 2001, p. 435).

Similarly, Raff (1996, p. 352) found it surprising "that both genes and principles of appendage development are shared between two phyla," i.e., arthropods (*Drosophila*) and vertebrates (tetrapods). As summarized by Wagner (1994, p. 275), organs with the same structural organization (structurally identical body parts) may have different developmental pathways, may use different genetic information for their development, and may not share a common phylogenetic origin.

Developmental biologists therefore recognize different concepts of homology, of which the one discussed in the preceding section – the phylogenetic or "taxic" concept of homology – is only one. In addition, there is the "morphological homology concept" that uses "structural identity for its definition," and the "biological homology concept," which is based on "shared developmental constraints" (Wagner 1994, p. 174; Roth 1984 emphasized shared developmental pathways instead). According to the latter concept, "structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype" (Wagner 1994, p. 275; see also Wagner 1989).

In contrast, West-Eberhard (2003, p. 486) distinguished what she called "broad-sense homology" (corresponding to "biological homology") from "cladistic homology." In contrast to cladistic homology, broad-sense homology allows for parallelisms (see the discussion above on the problem of an empirical distinction of parallelisms from taxic homology) and the recurrence of features previously lost in phylogeny. As such, broad-sense homology includes cladistic homology as a subset, the two concepts in fact representing "complementary approaches to understanding the evolution and stability of structure" (West-Eberhard 2003, p. 488; on the issue of complementarity, see the discussion later). Indeed, statements of biological homology and statements of phylogenetic (taxic, cladistic) homology may be expected to be congruent if the developmental mechanisms underlying the corresponding structures are so complex that their repeated evolution would seem very unlikely (Shubin 1994, p. 206). However, because of the problems outlined previously, "there is no rigorous way in which biological homology concepts can be used to distinguish between phylogenetic homology and homoplasy" (Shubin 1994, p. 206). It is for these reasons that comparative studies of development "can be used to trace homology, but developmental differences do not negate it" (West-Eberhard 2003, p. 496). Similarity of gene expression patterns and developmental pathways as captured by biological homology may support hypotheses of taxic homology but not the other way around (Rieppel 2004c).

Partial Homology or Partial Reference?

If true that development is a "process of *construction* and *reconstruction* in which heterogeneous resources are contingently but more or less reliably reassembled for each life cycle" (Oyama et al. 2001, p. 1), a situation might arise in which a developmental biologist would want to invoke a concept of partial homology.

The concept of modular development (Raff 1996; West-Eberhard 2003; for a review and references, see Rieppel 2004c) builds on connectivity yet dissociability of developmental modules. If developmental modules are dissociable, they can potentially "be reorganized somewhat independently of each other" (West-Eberhard 2003, p. 60), thus providing the resources for reassembly of traits derived from heterogeneous resources in descendant life cycles. Such "mosaic development" results in heterochrony, heterotopy, and other effects (Raff 1996) that led West-Eberhard (2003, p. 60) to speak of homology as "not an all-or-nothing phenomenon but rather a continuum of more or less similarity due to common ancestry." This conclusion, startling from a systematist's point of view, would seem to be supported by Raff's (1996) review of appendage development in *Drosophila* and tetrapods. Why not speak of partial homology of appendages in those widely separated lineages in which "appendages have a deep underlying and (prior to the findings of developmental genetics) completely unexpected homology" (Raff 1996, p. 353; see also Shubin et al. 1997; Gilbert and Bolker 2001)? Very basal building blocks are used to develop vastly different structures. But is it true that through such mosaic development, "evolution makes a mess of homology" (West-Eberhard 2003, p. 497)? Such a conclusion seems subject to a naturalistic fallacy. Homology is a theoretical concept. It may, indeed, be the case that our theoretical concepts are somewhat messy, but this is not because of evolution. The evolutionary process just unfolds the way it does, and this may be a way that is difficult to capture conceptually.

The call for partial homology can have two sources: the heterogeneous combination of ancestral resources in descendant life cycles as outlined previously or gradual and continuous morphological change as in Sattler's (1990, 1996, and references therein) "continuum morphology," which essentially reduces structure (s) to process(es). Although at odds with cladistics, Weston (2000, p. 141) considered it an avenue toward holism if partial homology was fitted as a distance measure on a tree. Why this appeal to holism?

The corollary of "continuum morphology" is that it "acknowledges gradations between typical structures . . .. From this point of view, homology is a matter of degree" (Sattler 1996, p. 577). The tension identified by Sattler (1990, 1996) between "typical structures" and the "continuity of developmental processes" broadly corresponds to the tension between "evolution and stability of structure" that was used by West-Eberhard (2003, p. 488) in support of her claim for complementarity. Indeed, the contrast between pattern and process can quite generally be conceptualized in terms of complementarity (Rieppel 1988), although this may in turn result in some tension with scientific realism that adheres to ontological monism. Ontological monism holds that there is one, and only one, way to carve nature at its joints, i.e., that particles and waves are not two different kinds of light but rather a reflection of our imperfect understanding of light. Accordingly, McMullin (2002, p. 252) argued that complementarity invoked in physics does not also invoke an ontological dualism, but rather points to the issue of partial reference of the terms deployed in complementary theories. The same seems true for biology.

The discussion of partial homology in terms of morphological stasis versus continuity of developmental change mirrors the paradoxical discussion of "species" as spatiotemporally delimited chunks of a genealogical continuum. With respect to species, Hey (2001, p. 168) found that “systematists and evolutionary biologists have both placed incommensurable demands on a word,” in which the word “species” is supposed to function in the context of pattern as well as process analysis (Hull 1997), and the same is true of homology. But again “a tendency for different perspectives by different biologists [must not] be confused with different kinds of reality” (Hey 2001, p. 150). Indeed, if species transformation is a gradual process, any species concept will be subject to the “sorites paradox” (Rieppel 2003b): take a heap of sand and remove grains one by one – when would one stop calling it a “heap”? Under the paradigm of gradualism, species boundaries will be unsharp, fuzzy, no matter which concept is deployed in their delineation (Hey 2001). The same is true of homology in cases in which morphological transformation (developmental and phylogenetic) is a gradual process. There is, however, a conceptualization of species that specifically allows for such fuzziness, which is that of homeostatic property cluster natural kinds (Boyd 1999; see also Griffiths 1999; Wilson 1999; Keller et al. 2003). The same concept can be applied to homologs, as was discussed previously (Rieppel 2004c). The conclusion is not that evolution makes a mess of homology but that it is the names associated with the natural kind terms (predicates) we deploy in statements of homology that may have imprecise, or even only partial, reference (the terms apply only imprecisely, or partially, to the organisms under analysis).

A second issue to consider in relation to the concept of partial homology is the fact that natural kinds, such as taxa or homologs, come in hierarchies and thus raise the *qua* problem for natural kind terms as discussed previously (Devitt and Sterelny 1999). The statement “bird wings and bat wings are homologous” makes little sense unless it is tied to a conditional phrase. The same is true of the statement “arthropod and tetrapod appendages are partially homologous,” unless the question is raised in which sense they are homologous, partially or not. The concept of partial homology may reflect a tendency of developmental biologists to use broad-sense homology independent of a hierarchical conception of development. If the sense of partial homology in this example relates to certain gene expression patterns (a “similar genetic cascade”) (Shubin et al. 1997, p. 646), then the homology relation exists not at the level of appendages, but at the level of genes, which ties the homology relation to its proper hierarchical level. Gilbert and Bolker (2001, p. 447) speak of such gene-level homology as “deep homology,” for insect “legs” and vertebrate “legs” obviously cannot be homologous as appendages, because “phylogenetically intermediate taxa (particularly basal chordates) do not possess comparable structures” (Shubin et al. 1997, p. 645). However, Gilbert and Bolker (2001, p. 449) added a note of caution to this tale of wings and legs. Applying the “small toolbox argument” to developmental processes in the name of parsimony, they draw attention to the fact that genetic resources that regulate basal (early) patterning processes in development are limited, for which reason convergent gene expression patterns are difficult to rule out. For example, much of the “toolbox” that is involved in early limb development is also involved in the early development of vertebrate teeth.

Taxic Versus the Transformational Approach to Homology

The phylogenetic literature that deals with species, taxa, as well as with homologs, is replete with dismissals of taxa, or homologs, as natural kinds, for these are considered abstract entities, like sets, or classes (Hull 1999). The same is true of properties (attributes), which are dismissed as universals that cannot be instantiated by evolutionary entities (Grant and Kluge 2004). Hey (2001, p. 153), for example, dismisses property cluster kinds as polythetic classes, where "a polythetic class is just a category in which the members need only meet some, not all, of the membership criteria." But as emphasized previously, for property cluster kinds (as well as for other kinds) to be natural requires that their properties are relevant to causal processes, i.e., that tokens of kinds take part in causal processes by virtue of their properties (Sober 1981; Boyd 1999; Shoemaker 2003; La Porte 2004; Lipton 2004).

Homologs (Grant and Kluge 2004), as well as species (Hull 1999), have been considered to be particulars (individuals). This move was motivated by a certain reading of Hennig (1950, 1966), which found him to have replaced "intensional" with "extensional" thinking in systematics (Dupuis 1984). Such reading of Hennig has led to the assertion that systematics must rely on "ostension" and "extensionality" (Kluge 2003a). The meaning of extensionality as used in this context remains obscure (Dupuis 1984, p. 13: "Hennigian taxonomy is extensional since, for appraisal of each attribute, it requires an extensive consideration of various objects"), whereas the relation of ostension is more easily understandable. In the simplest case, ostension is the relation of "pointing at" an object in order to establish that object as the referent of a proper name or of a sentence of the subject-predicate structure (Fx). But for Grant and Kluge (2004), it is not objects and their properties that serve as homologs. Instead, "only the transformation from one character state to another, $a \rightarrow a'$, constitutes evidence in phylogenetic inference" (Grant and Kluge 2004, p. 25). If only transformation events constitute evidence, and if systematics is to be ostensional, then systematists would have to be able to "point at" such transformation events. The collapse of a bridge or the burning of a house are events that witnesses can point at, but the transformation events that are of interest to systematists are events of the past. What is required, therefore, is identification of character states and inference of their transformation. "However, character state transformation has always been treated primarily as a metaphor .... Furthermore, character states themselves can be seen as manifestations of the transformational metaphor" (Weston 2000, p. 135). In this quote, I would replace the term "metaphor" with that of "concept," for as convincingly argued by Hanson (1961), perception itself entails a conceptual component (Rieppel 2004a). As noted earlier, the mere pointing at a rabbit and the utterance of "gavagai" by a native speaker does not tell the English-speaking audience what the native speaker means by gavagai: a rabbit, an undetached rabbit part, or a rodent (Quine 1964)? It seems impossible to meaningfully talk about the world without concepts (Luntley 1999).

A transformation series of character states purported to be homologous does not result from mere ostension but from character conceptualization ("transformation series analysis . . . begins with the *construction* of an initial transformation series": Kitching et al. 1998, p. 218; my emphasis). Hennig (1966, p. 94) was very clear on this issue: "the belonging of characters to a phylogenetic transformation series . . . cannot be directly determined." To solve the problem, Hennig (1966, p. 94) turned to an account (in Cain and Harrison 1958, pp. 86–88) of J.H. Woodger's analysis of morphological comparison in the language of logical positivism (Rieppel 2003b), which "to that extent is exact" (Hennig 1966, p. 94). According to Woodger (Cain and Harrison 1958), morphological comparison individuates parts of organisms in terms of their relation and compares them in terms of their properties. The description of properties of, and relations between, objects is the cornerstone of the positivist philosopher Rudolf Carnap's "construction theory," i.e., the theory of how science reconstructs the logical structure of the world (Mayhall 2002). As argued earlier, the same theoretical background underlies Hennig's (1957, 1966) conceptualization of the cladogram (Rieppel 2003b). There is no need to look back on Carnap, Woodger, or even Hennig, however, to understand that the identification of characters, character states, and transformation series entails a conceptual component (Hanson's (1961) work was, after all, a stab at the positivists' adherence to something akin to "simple" observation). In his talk announcing his own transformation, Farris (Mitter 1980, p. 188; see also Dupuis 1984, p. 16) asserted that "morphologists do not sample characters, they synthesize them." If "extensional" systematics must be based on ostension, but if it admits only character transformation as evidence, then the argument boils down to the claim that systematists must be able to "point at" concepts. This conclusion merely shows that such arguments confound concepts with objects (Mahner and Bunge 1997).

The discussion of transformation series reflects back on the "transformational" versus "taxic" approach to homology that was hinted at by West-Eberhard (2003) in her distinction of broad-sense versus cladistic homology. The essence of this debate (that started with Patterson 1982) is that the transformational approach allows homology to encompass both symplesiomorphy and synapomorphy, whereas the taxic approach requires homology to be synonymous with synapomorphy (it requires a statement of homology to be coextensive with a statement of synapomorphy). Wiesemüller et al. (2003, p. 89) consider the taxic approach as too coarse-grained because it blurs the distinction of plesiomorphy and apomorphy, in addition to the fact that the concept of homology cannot easily be applied to "absence" – characters. The latter problem was (arguably) "solved" semantically: snakes do not have "no legs," but instead they have "modified legs," i.e., "lost legs" (Platnick 1978; see the discussion of the deduction of different meanings from different premises in Rieppel 2004b, p. 79). The distinction of homology from symplesiomorphy and synapomorphy on the other hand is related to the *qua* problem. "Bird wings and bat wings are homologous" violates the requirement for coextensionality of statements of homology and of synapomorphy because it implies a symplesiomorphy: birds and bats share tetrapod (fore)limbs, not wings.

Patterson's (1982) goal simply was to remove ambiguity and render statements of homology testable by congruence, in claiming that homology statements should always be assessed as (*qua*) statements of synapomorphy – since what is a symplesiomorphy at one level (jaws of amniotes) becomes a synapomorphy at a more inclusive level (jaws of gnathostomes). An interesting evolutionary talk about a comparison of bird wings with bat wings would be a talk about convergence, but then bird wings and bat wings could not be homologous.

Conclusion

Homology is one of two perennially discussed topics in comparative biology – the other is species. The two discussions show many parallels, as indicated previously: proper names versus general names, individuals versus classes, sets, or kinds. To turn homologs into individuals and anatomical (or molecular) terms into proper names (Grant and Kluge 2004) is patterned on the argument that species are individuals (e.g., Hull 1999). This latter argument has received a lot of attention from evolutionary biologists, who largely missed an important part of its theoretical foundation. In his defense of the argument from a philosophical point of view, Hull (1976, p. 179, n. 4) drew attention to the semantic behavior of species names in evolutionary theory, which in his analysis corresponds to the semantic behavior of proper names as "rigid designators" (Kripke 2002). Such behavior of proper names is tied to a specific theory of reference for proper names, i.e., the "historical," "causal," or "direct" theory of reference (Hull 1976, p. 179, n. 4; see also Hull 1988). These are all rather technical issues that need not be reviewed here; there is also no need to deliver a verdict on the ontological status of species here. The important point is that authors who want to use – in an evolutionary context – the "names" that refer to "the same organ in different animals under every variety of form and function" as proper names will need to worry about those technicalities but have not done so far.

In the present context, homology is conceptualized in terms of natural kind term semantics, and the names associated with natural kinds can be general names or singular terms (Soames 2002). Kripke (2002) himself already expanded his theories to also apply to natural kind terms, such as "tiger," "water," or "gold," but as noted by Devitt and Sterelny (1999), the use of such terms – at least in the case of biological natural kinds – at some level involves some descriptive account (for Kripke 2002, a descriptive account may help to fix reference, but does not determine reference, of proper names or natural kind terms). This means that the use of names (associated with natural kind terms) to refer to "the same organ in different animals under every variety of form and function" must be tied to a conditional phrase that specifies the hierarchical level at which the use of that name gains some cash value in terms of marking out monophyletic groups. This in turn means that phylogeny reconstruction cannot be a matter of mere extensionality and ostension (Kluge 2003a, b; Grant and Kluge 2004), but requires a conceptual, i.e., a theoretical framework. There is no immediate access to objective reality, but this only means that careful phylogenetic analysis will require at least an attempt to causally ground hypotheses of homology, proximally in criteria of topology and connectivity, ultimately in the theories of inheritance, development, and evolution.

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Chronometric Methods in Paleoanthropology

Daniel Richter and Guenther A. Wagner

Contents

Abstract

Chronometry or numerical dating aims to provide age estimates in terms of years for archaeological and paleoanthropological events or processes. Most of the methods currently applied with success are based on the physical phenomenon of radioactivity, which provides the clock. Ongoing developments in the last few decades provide rapid progress in the growing field of chronometric dating. In particular, improvements in time resolution and application to novel sample materials as well as the extension of the age ranges have left a strong impact on

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D. Richter (✉)
Department of Human Evolution, MPI Evolutionary Anthropology, Leipzig, Germany

LS Geomorphology, University of Bayreuth, Bayreuth, Germany
e-mail: drichter@eva.mpg.de

G.A. Wagner
Geographisches Institut, Universität Heidelberg, Heidelberg, Germany
e-mail: gawag-wagner@web.de; guenther.wagner@cez-archaeometrie.de

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current paleoanthropology. This contribution introduces the reader to the principles of radiometric dating. The most frequently applied dating methods, such as potassium–argon, uranium-series, luminescence, electron spin resonance, cosmogenic ^{26}Al/^{10}Be, and radiocarbon techniques, are described. Their potential for paleoanthropology is illustrated using various examples covering the entire period since hominini entered the scene a few million years ago.

Introduction

In paleoanthropology – as in any historically oriented discipline – the *time* when something happened is fundamental. The recorded events are by themselves poorly informative until they are arranged in their correct chronological order. Once such an order is established, a mutual causal relation between the events may be confirmed or rejected. For instance, the coexistence of Neanderthals with modern humans excludes any hypothesis of simple evolution of the former into the latter within the given geographical area. Furthermore, a firm chronological database enables assessing the duration and the rate of processes, as in the case of the remarkably fast spread of *Homo erectus* out of Africa. It is for these reasons that the rapid progress that chronometric dating has experienced during the past few decades has substantially fostered the development of modern paleoanthropology.

Chronometry refers to the measurement of past time in terms of years and provides numerical age results. Before the introduction of chronometric dating to the field of prehistory, age determination relied essentially on the principles of stratigraphy, which reveals merely relative datings. A turning point came with the development of radiocarbon dating around 1950, soon followed by potassium–argon and other dating techniques. Nowadays, several chronometric dating methods are available, based on physical phenomena. Since the result of a physical measurement represents only a more or less accurate approximation of the sought-after true value – which is and which remains unknown – the often used term "absolute" dating seems inappropriate and should be avoided. Instead, the terms "chronometric" and "numeric" dating are recommended. The estimated deviation of the measured age value from the true one is given by the uncertainty. The uncertainty $\pm \sigma$ describes an interval from $(t-\sigma)$ to $(t + \sigma)$ surrounding the calculated age t, which is usually the mean of multiple measurement results. Within this confidence interval, the true value is expected at a certain probability. Consequently, the uncertainty is an integral part of the age result and must not be omitted in interpretation and discussion. In interpretation it is essential to use a high probability (95.45 %, i.e., $\pm 2\sigma$) to bolster confidence that the "true" age lies within the age range given, by subtracting and adding 2σ from the mean age provided. Here it is essential to note that the "true" age can lie anywhere within this range; and when comparisons are made, age results with overlapping ranges have in general to be considered as statistically being of the same age.

While understanding that chronometric dating results provide a probability range, and not a single "true" value, it is also important to consider the relationship between the event dated and the event being addressed (Dean 1978). Dating an associated bone determines the time of decease of the organism; and only by inference can it be concluded that, say, the deposition of an artifact is contemporaneous with the death of the animal dated. It is very rare to date an event that is directly related to remains of hominine or human manipulation of objects. In many cases, ages have to be established by correlations, sometimes based on series of logical arguments, which are obviously less strong than direct dating.

In numerical dating a "clock" is required, i.e., natural time-dependent processes that lead to quantifiable changes within prehistorical time scales, whereby the rate of the process needs to be known. Furthermore, the process must be either started or reset – like a stopwatch – at the moment of interest to the paleoanthropologist. For example, in case of stone artifacts, it is not the age of the rock itself but that of manufacture or use which is of interest. Processes fulfilling these requirements are rare, but the discovery of radioactivity by Henri Becquerel in 1896 provided an avenue to knowledge of such processes. Because radioactive decay is a property of the atomic nucleus, its decay rate is insensitive to ambient parameters such as temperature, pressure, and chemical bonding. The radioactive clock thus runs steadily, regardless of environmental influences. Because of this unique property, radioactivity may aptly be called the "mother of chronometry."

A *nuclide* is an atomic species characterized by its numbers of nuclear protons and neutrons. Their sum is the mass number, which is indicated as superscript to the upper left of the element symbol. For example, the nuclide ^{14}C consists of six protons, which define the element carbon, and eight neutrons. Nuclides belonging to the same element are called *isotopes*, which means that they have the same number of protons but different mass numbers, such as the three carbon isotopes ^{12}C, ^{13}C, and ^{14}C. Most natural nuclides are stable, but others disintegrate spontaneously – a phenomenon called *radioactivity*. The rate of this disintegration is nuclide characteristic. The radioactivity dN/dt (in the unit of *Becquerel Bq* [s^{-1}]) is defined as the fraction dN of the radioactive parent nuclide N (with initial amount N_0) that disintegrates within the time interval dt into the radiogenic stable daughter nuclide D ($= N_0 - N$)

$$\frac{dN}{dT} = -\lambda \cdot N = -\frac{\ln 2}{t_{1/2}} \cdot N \tag{1}$$

where by λ [a^{-1}] is the decay constant and $t_{1/2}$ [a] the half-life ($= 0.693/\lambda$).

By integration one obtains the equation

$$\frac{N}{N_0} = e^{-\lambda \cdot t} \tag{2}$$

and substituting (D + N) for N_0

$$\frac{D}{N} = e^{\lambda \cdot t} - 1 \tag{3}$$

The age t [a] can be derived, depending whether N_0, N, or D is known, according to one of the following equations:

$$t = \frac{1}{\lambda} \cdot \ln\left(\frac{D}{N} + 1\right) \tag{4}$$

$$t = \frac{1}{\lambda} \cdot \ln\left(\frac{N_0}{N}\right) \tag{5}$$

The use of a radioactive system for age determination presupposes that neither the parent nor the daughter nuclides are lost or gained except through the decay process itself – a condition that is known as *closed system.*

There are several types of radioactive decay: α-decay takes place under emission of an α-particle, which is a ^{4}He nucleus. During β-decay the nucleus emits a β-particle, which is an electron, whereby a neutron is converted into a proton. Electron capture occurs when the nucleus captures an extra-nuclear, orbiting electron from the innermost atomic shell (K-shell) whereby a nuclear proton is converted into a neutron. During spontaneous fission, the atomic nucleus splits into two heavy fragments and 2 or 3 neutrons. Some nuclides exhibit a dual decay mechanism, as α-decay and spontaneous fission for ^{238}U. Radioactive decay is generally accompanied by the emission of energy-discrete γ-rays, which are a type of electromagnetic radiation from the exited nucleus.

Instead of being stable, the daughter nuclide may be radioactive and disintegrate itself. Several such radioactive daughter nuclides may be following each other to form a decay chain until finally a stable end product is reached. Most prominent for chronometric dating is the decay chain starting from ^{238}U and ending at ^{206}Pb involving several steps of α- or β-disintegration. If the decay chain stays undisturbed, i.e., under closed-system conditions, a balance between production and decay of the interim members is gradually established. At this stage, which is called radioactive or secular equilibrium, all radioactive members N_1, N_2, N_3, etc., assume equal radioactivity dN/dt.

$$\lambda_1 \cdot N_1 = \lambda_2 \cdot N_2 = \lambda_3 \cdot N_3 \ldots \text{etc.} \tag{6}$$

In nature various kinds of radioactive nuclides occur, and many of them can be used for chronometry. Due to their origin, these nuclides can be divided into various groups: *Primordial nuclides* are left over from the time of nucleosynthesis and, thus, are older than the formation of the Earth (e.g., ^{238}U). *Radiogenic nuclides* are produced by radioactive decay (e.g., ^{230}Th). *Cosmogenic nuclides* are formed by the interaction of cosmic rays with the atmosphere and the Earth's surface (e.g., ^{14}C). *Anthropogenic nuclides* are produced in nuclear plants and explosions (e.g., ^{3}H). For the Quaternary period, there is a wide spectrum of dating methods available (Wagner 1998; Walker 2005; Taylor and Aitken 1997; Noller et al. 2000), and the following presents an outline of the radiometric dating methods (Fig. 1) with sound paleoanthropological potential.

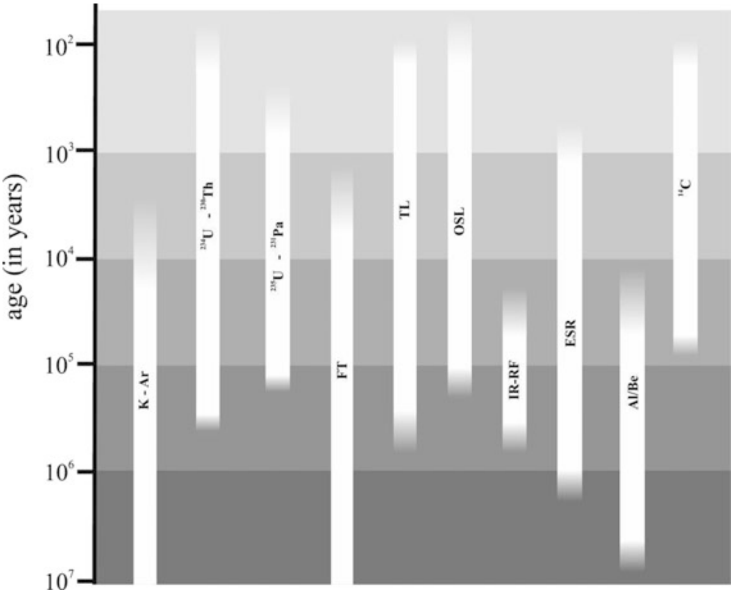

Fig. 1 Important radiometric dating methods for the Pliocene/Pleistocene period with their application ranges

In addition to chronometric application at sites, such methods are also used for relative dating by providing numerical ages for calibration or as anchor points. The relative dating method of paleomagnetism (e.g., Gubbins and Herrero-Bervera 2007) is important in paleoanthropology. It employs the directional changes of the Earth's magnetic field (reversal of polarity), which is synchronously recorded in rocks or deposits during their sequential formation. Such worldwide events can be numerically dated at one location, and an age is therefore provided for all other sites where this event is detected. This is especially useful for sites which cannot be dated by chronometric methods, but it also provides further evidence of the age of sites or sequences and is also employed as a verification/falsification tool.

Potassium–Argon

The K–Ar method covers the whole age range from the beginning of the solar system to the Holocene and has become undoubtedly one of the most important chronometric dating tools since the first attempts by Smits and Gentner (1950). The term "potassium–argon" stands for several dating techniques. Apart from the conventional K–Ar technique ($^{40}Ar/^{40}K$), these are the argon–argon ($^{40}Ar/^{39}Ar$) and the argon–argon laser techniques. In particular the latter ones play a crucial role in Pliocene/Pleistocene geochronology whenever volcanic materials are involved.

All techniques are based on the same phenomenon: the radioactive decay of the potassium isotope ^{40}K into the argon isotope ^{40}Ar. In its relation to the potassium content, the amount of accumulated radiogenic argon becomes a measure for the age. The various techniques essentially differ in their analytical and gas extraction procedures.

Potassium is the eighth most common element in the Earth's crust and occurs widely in rock-forming minerals such as feldspar and hornblende. One of its three natural isotopes, ^{40}K, with an isotopic abundance of 0.01167 %, is radioactive. It disintegrates under electron capture, with a decay constant λ_e of 0.58110^{-10} a^{-1}, to the stable argon isotope ^{40}Ar. The long half-life of 11930 Ma implies that in the time span of a few Ka, only very low amounts of radiogenic $^{40}\mathrm{Ar}_{\mathrm{rad}}$ are produced. Thus, potassium-rich minerals, such as sanidine, are preferred in Quaternary applications. Recent developments in ultrasensitive analytical technology, however, allow the determination of ages as low as few thousand years. The clock provided by K–Ar is used to date events correlated with the last complete degassing. In Pliocene/Pleistocene contexts such events are essentially the solidification of minerals in relation to volcanic eruptions. Important materials are widespread tephra layers, for which K–Ar dating yields excellent tephrochronologic time markers, for example, tephras intercalated with early-hominid-bearing sediment layers.

The K–Ar-age t [a] is assessed under the assumptions that no $^{40}\mathrm{Ar}_{\mathrm{rad}}$ was present in the sample at the moment of the last degassing, which had to be complete, and that the subsequently produced $^{40}\mathrm{Ar}_{\mathrm{rad}}$ remained quantitatively in the sample. Argon is analyzed by mass spectrometry and potassium by atomic absorption. This technique is called *conventional K–Ar dating*.

Apart from radiogenic ^{40}Ar, there are contaminant sources of this isotope. Samples always contain more or less *atmospheric derived argon* $^{40}\mathrm{Ar}_{\mathrm{atm}}$, which must be subtracted from the total ^{40}Ar in order to obtain the radiogenic fraction $^{40}\mathrm{Ar}_{\mathrm{rad}}$. This correction is possible because of the known isotopic abundance of atmospheric argon $(^{40}\mathrm{Ar}/^{36}\mathrm{Ar})_{\mathrm{atm}} = 295.5$ and requires the measurement of the isotope ^{36}Ar in addition to ^{40}Ar. As a noble gas, argon is chemically inert and thus should be driven out of the crystal lattice during heating so that the K–Ar clock is reset. If the degassing is incomplete, an *extraneous ^{40}Ar* component is left in the mineral, resulting in an overestimation of the K–Ar age. Such non-atmospheric argon contamination needs to be identified and is accounted for in single-grain or isochron-dating techniques. The younger the rock, the less abundant is the radiogenic ^{40}Ar and the larger is the fraction from contaminant argon sources. Therefore, special K–Ar techniques which allow analyzing minute proportions of radiogenic argon have been developed for age determination of Quaternary samples.

After the resetting event, the K–Ar system must stay closed. Partial loss of argon results in an underestimate of the K–Ar-age value. The leaking of argon from minerals may happen continuously during weathering or episodically during thermal overprint. For unweathered Quaternary volcanites that cooled quickly after eruption to surface temperature, and stayed cool afterwards, argon loss is rare. If present, argon loss can be recognized and corrected by the step-heating *$^{39}Ar/^{40}Ar$ plateau technique*.

In the *^{39}Ar/^{40}Ar* technique, potassium is determined through a nuclear reaction instead of chemical analysis. The sample is irradiated with fast neutrons, whereby the argon isotope ^{39}Ar is produced from the main potassium isotope ^{39}K. The abundance of the artificial isotope ^{39}Ar is measured together with ^{40}Ar and ^{36}Ar by mass spectrometry. The age is determined against a standard of known age, which is irradiated jointly with the sample to be dated. This requires the measurements only of isotope ratios, and not explicit quantities, which improves accuracy. A further advantage of this technique over conventional K–Ar dating is the ability to recognize argon loss or extraneous argon. This is achieved by stepwise heating and differential degassing of the sample, whereby for each step, the ^{40}Ar/^{39}Ar ratio of the released argon is measured. In the absence of argon loss and of excess argon, the corresponding ages display the same age for the heating steps, which is called the plateau.

The *laser technique* is a variant of the ^{39}Ar/^{40}Ar technique in which the heating is achieved under a laser beam. The sample is either incrementally heated and finally fused – analogous to the plateau technique – or, without gradual degassing, directly fused and analyzed. The main advantage of this technique is its ability to analyze single grains in the sub-milligram range. The grain-discrete probing enables identifying contaminating detrital grain populations by their greater age.

To test whether the K–Ar system is disturbed by excess argon, the *isochron technique* is also used. It relies on cogenetic fractions from the same rock sample having different potassium contents. In the isochron diagram, ^{40}Ar/^{36}Ar is plotted against ^{39}Ar/^{36}Ar. All data points of the subsamples lie on a straight line (isochron) where the slope defines the age, and the intercept with the y-axis reveals the initial ^{40}Ar/^{36}Ar ratio, which exceeds the present atmospheric ratio of 295.5 in case of excess argon. ^{36}Ar/^{40}Ar versus ^{39}Ar/^{40}Ar diagrams are also employed, in which straight lines of negative slope define undisturbed systems. Usually isochron plots are applied in connection with laser single-grain analysis. In such cases it is important to probe a sufficiently large number of crystals in order to discriminate between xenocrysts (older crystals incorporated into the volcanic rock), phenocrysts (crystals that solidified from the volcanic melt before eruption), and the crystals formed during the volcanic eruption (Chen et al. 1996).

Of particular significance in paleoanthropology are widespread tephra horizons intercalated in sedimentary sequences. The eruption ages yield invaluable tephrochronologic and stratigraphic time markers. Current knowledge about the timing of hominid evolution rests essentially on K–Ar data from such tephra (Brown and McDougall 2011). However, tephra layers in sediments may be reworked and thus contaminated with mineral detritus of various provenances. In such cases, bulk K–Ar or Ar/Ar dating of mineral concentrates yields an integrated age which is not related to a specific volcanic eruption. For this reason, but also for the recognition as correction of excess argon, single crystal probing is required in order to identify the various components of different age. This is optimally achieved with the grain-discrete Ar/Ar laser technique. Suitable mineral phases are potassium-bearing feldspars, such as sanidine and plagioclase, but also biotite, hornblende, and acidic glass shards.

One of the most renowned sites with early hominin fossils is Olduvai Gorge, Tanzania. The ca. 100 m thick Pliocene/Pleistocene sediments contain numerous tephra horizons and lava flows. Remains of *Australopithecus boisei* were uncovered as well as stone tools in Bed I. Continuous efforts to date this bed had aroused controversial views on *Homo habilis* and its age. Finally, single-grain ^{40}Ar/^{39}Ar laser-fusion dating succeeded in establishing a detailed and reliable chronology (Walter et al. 1991). Feldspar-grain populations of different ages were observed, allowing the decisive tuff component to be distinguished from older, reworked contamination. The weighted means of single grains from this juvenile component are 1.798 ± 0.004 Ma for Tuff IB and 1.779 ± 0.007 Ma for Tuff IF, located within sedimentary layers that include the fossil hominids. The oldest Oldowan-type stone tools, discovered at Gona, Ethiopia, have an age of 2.6–2.5 Ma. They are associated with cut-marked bones. The dating of the artifact-bearing layer is based on an overlying tuff, which yielded 2.53 ± 0.15 Ma as weighted mean of single-plagioclase ^{40}Ar/^{39}Ar ages, and the underlying Gauss–Matuyama paleomagnetic boundary, which is placed at 2.58 Ma (Semaw et al. 2003). Even older use of stone artifacts is postulated by the presence of cut marks on bones from sedimentary deposits dated by ^{40}Ar/^{39}Ar on intercalated tephra to 3.39 Ma at Dikika in Ethiopia (McPherron et al. 2010). The interpretation as well as the association, however, was challenged (Domínguez-Rodrigo et al. 2012). While the consumption of animal tissue certainly predates the use of stone tools, it has to be acknowledged that marked bones might be more informative on early stone use than the stones themselves, the anthropogenic origin of which might be much more difficult to identify.

At the Pliocene site of Fejej, Ethiopia, with dental remains attributed to *Australopithecus afarensis*, the fossil-bearing sandstone is capped by fine-grained basalt flows. Whole rock samples from the two lowest basalt outcrops were analyzed with the laser ^{40}Ar/^{39}Ar incremental-heating technique. Both samples provided long age plateaus from which mean ages of 3.94 ± 0.05 Ma and 4.06 ± 0.07 Ma, respectively, were calculated. When combined with paleomagnetical data from the site, a minimum age of 4.00–4.18 Ma was assigned to the fossil teeth, making them some of the oldest remains of *Australopithecus afarensis* (Kappelman et al. 1996).

As to the question of the origin of *Homo erectus* (sensu lato), K–Ar data are of special interest. The earliest fossil trace of this species in Africa occurs in the Koobi Fora region, Kenya. Based on K–Ar dating (McDougall 1985), an age of 1.8–1.9 Ma is assigned by interpolation (Feibel et al. 1989). According to K–Ar evidence, *Homo erectus* seems to have appeared at almost the same time in Western Asia. At Dmanisi, Georgia, fluvio-lacustrine sands with several hominid remains assigned to this archaic species are directly under- as well as overlain by volcanic flows and ashes. This stratigraphic situation allows the application of ^{40}Ar/^{39}Ar age bracketing, resulting in 1.85 ± 0.1 Ma and 1.81 ± 0.05 Ma for the lower and upper volcanic events, respectively (de Lumley et al. 2002). The morphology of these early Dmanisi *Homo erectus* appears primitive. Based on ^{40}Ar/^{39}Ar laser-incremental ages (1.81 ± 0.04 Ma and 1.66 ± 0.04 Ma) on hornblende, separated from pumice of two *Homo erectus* (*Pithecanthropus*) sites in Java, Swisher et al. (1994) claimed that *Homo erectus* appeared concurrently in Southeast Asia. However, the stratigraphical position of the former hominid finds seems to be above the dated pumice, so that these ^{40}Ar/^{39}Ar ages can be considered merely as a *terminus post quem* for these hominids in Java (Semah et al. 2000). Still, *Homo erectus* appears not much later on Java, because a recent find can be dated with an ^{40}Ar/^{39}Ar plateau age of 1.51 ± 0.08 Ma on epiclastic pumice, located stratigraphically slightly above and in close proximity to the in situ find spot of a maxilla (Zaim et al. 2011). The current sparse evidence of morphology and numeric dating actually allows currently opposing interpretations of *Homo erectus* moving from Asia to Africa, as well as from Africa to Asia (Wood 2011). Nevertheless, several *Homo* species roamed Africa after 1.95 Ma, with most of the dating evidence provided by Ar/Ar (Leakey et al. 2012).

For the emergence of anatomically modern humans, the discovery of fossil *Homo sapiens* at Herto, Ethiopia, in fluvial and lacustrine sandstone with Lower and Middle Stone Age technocomplexes is of prime importance (Clark et al. 2003). The upper age limit for this sandstone unit was determined by ^{40}Ar/^{39}Ar incrementally heated multigrain analysis of anorthoclase from embedded pumice, yielding 163 ± 3 Ka and 162 ± 3 Ka, respectively, and of embedded obsidian clasts, yielding 160 ± 2 Ka. The lower age is constrained by the ^{40}Ar/^{39}Ar laser-fusion mean age of 154 ± 7 Ka of single grains from the juvenile sanidine component separated from a tuff which caps the fossiliferous unit elsewhere, but is correlated by a series of stratigraphical and isotopic arguments. While these data provide evidence for the out-of-Africa model of *Homo sapiens* origin, the lack of chronometric evidence for the fossil-bearing layer has led to questioning the proposed minimum age (Faupl et al. 2003 vs. Hart et al. 2003). Similarly, the other unequivocally anatomically modern human from Omo Kibish (Ethiopia) is dated by correlation of various tephra deposits and stratigraphical lines of arguments. Again, ^{40}Ar/^{39}Ar dating of these correlated pumices provides numerical age estimates, which all together place the age of these human remains at ca. 196 Ka (Brown et al. 2012). But they do not give direct age estimates for the human fossil nor for the fossil-bearing deposit.

Uranium Series

This general term comprises several closely related dating methods based on the radiometric disequilibrium within the radioactive decay series arising from the two uranium isotopes ^{238}U and ^{235}U (Ivanovich and Harmon 1992). The terms decay series, disequilibrium, or uranium–thorium methods of dating are also occasionally used. In paleoanthropology the ^{230}Th/^{234}U method is mostly applied, with a dating range to about 400 Ka in age, but U/Pb dating has been used as well (e.g., de Ruiter et al. 2009; Balter et al. 2008). Of particular interest for ^{230}Th/^{234}U dating are secondary carbonates of caves and springs and to a lesser degree also fossil teeth and bones. Occasionally the ^{231} Pa/^{235}U method is applied, up to 150 Ka.

The uranium-isotope ^{238}U, which constitutes 99.3 % of natural uranium, is radioactive and decays over a chain of intermediate radioactive daughter nuclides to the stable lead-isotope ^{206}Pb. In closed systems, equilibrium develops with time among all radioactive nuclides within the decay chain. In the state of radioactive equilibrium, all radioactive nuclides possess equal activity (Eq. 6). In nature, most minerals and unweathered rocks represent closed systems, in which radioactive equilibrium persists simply as a result of their geologically large ages. If such a system is disturbed, it will take some time, practically five half-lifes, until the daughter nearly returns to equilibrium with its parent nuclide. For the system ^{230}Th/^{234}U, in which ^{234}U decays by α-emission to ^{230}Th, disequilibrium arises through geochemical fractionation. Uranium is readily dissolved in groundwater and available for uptake by secondary carbonates as well as by dental/bone tissue. Thorium, on the other hand, preferentially stays adsorbed to mineral particles and thus is not easily dissolved in groundwater. Consequently, fresh calcareous deposits incorporate uranium but not thorium, that is, $(^{230}\mathrm{Th}/^{234}\mathrm{U})_{t=0} = 0$. During the following 400 Ka, corresponding roughly to five times the ^{230}Th half-life of 75.6 Ka, the ^{230}Th/^{234}U system gradually builds up to equilibrium. The time-dependent increase of ^{230}Th/^{234}U enables the determination of the time t elapsed since the event of disturbance, which equals here the precipitation of the mineral.

The essential requirements for dating are the negligibly small (or known) initial abundance of the daughter product (^{230}Th), and that after the disturbance, the radioactive system is/remains closed. Complications in ^{230}Th/^{234}U dating have various sources: (1) During incorporation ^{234}U is not necessarily in equilibrium with its radioactive predecessor ^{238}U, since in groundwater the activity ratio is $^{234}\mathrm{U}/^{238}\mathrm{U} > 1$, so that the ^{234}U/^{238}U ratio must be determined and taken into consideration for age calculation. (2) The requirement that the investigated material is free of ^{230}Th is frequently not fulfilled since thorium, and consequently also ^{230}Th, may be present. Negligible ^{230}Th contamination is indicated by $^{230}\mathrm{Th}/^{232}\mathrm{Th} > 20$. (3) The system may experience a secondary opening as a result of the geochemical mobility of the uranium.

Originally the activity of the Th and U isotopes was analyzed by α-spectrometry. The introduction of thermo-ionization mass spectrometry (TIMS) by Edwards et al. (1986/87), which requires less than 1 g of sample material and provides high age precision, brought a great impetus for ^{230}Th/^{234}U dating. More recently multicollector inductively coupled plasma mass spectrometry (MC-ICPMS) has been used. This can additionally provide spatial information when coupled with laser ablation (LA-MC-ICPMS), but at the cost of precision compared to solution MC-ICPMS or TIMS. Under favorable circumstances, age precisions better than 1 % can be obtained. The uranium content should be more than 0.1 μg g^{-1}. When sampling, e.g., *speleothems* (calcareous flowstones formed on the cave floor), dense and pure carbonates should be collected in order to minimize potential problems, i.e., open-system behavior and ^{230}Th contamination by detrital components.

This was carefully investigated in the dating of very thin secondary carbonate crusts, which had developed on top of Upper Paleolithic rock art or was already present at the time of the creation of the art. The resulting U-series ages obviously can provide only *ante quem* and *post quem* dates for the rock art, with uncertainties below 2 % at the 95 % confidence limit. It was shown that European rock art dates back to the Early Aurignacian period, with a minimum age of 40.8 Ka (Pike et al. 2012). Artwork therefore appears to have already been part of the repertoire of *Homo sapiens* when colonizing Europe at this time, or shortly beforehand, as also evidenced by painted stones and elaborate figurative art in southern German caves (cf. TL and radiocarbon dating).

In the Tongtianyan Cave, Guangxi, China, one of the few Pleistocene fossils of *Homo sapiens* in Asia was discovered. Several speleothem layers, intercalated in the cave sediments, were dated by ^{230}Th/^{234}U. The age results of 13.5 ± 2.3 Ka, 63.1 ± 2 Ka, and 148 ± 4 Ka, for three layers from top to bottom, follow the stratigraphical order (Shen et al. 2002). Although the stratigraphic position of the hominid find is to some extent uncertain, it was certainly located below the second layer. This renders this find as one of the earliest in East Asia, indicating that modern humans arrived there before ca. 60 Ka ago.

Depending on the measurement precision, the ^{230}Th/^{234}U system in speleothems older than 350 Ka often shows equilibrium, so that only a *terminus ante quem* can be given for the age. This situation was met in the fossil hominid sites known as the Sima de los Huesos, Spain, and the Caune de l'Arago, France. At Sima de los Huesos, the numerous human individuals, which are considered as evolutionary ancestors of the Neanderthals, are overlain by a speleothem in equilibrium and thus older than 350 Ka (Bischoff et al. 2003). Analogously, the pre-Neanderthals found in the Middle Pleistocene unit III at Caune de l'Arago have to be older than 350 Ka (Falguères et al. 2004). At the famous Zhoukoudian site near Peking, yielding the *Homo erectus* commonly known as Peking Man, speleothems which were intercalated in the fossiliferous sediments were ^{230}Th/^{234}U dated. In most samples the ^{230}Th/^{234}U system was close to equilibrium. However, high-precision analysis of these nuclides enabled to push the dating method to its upper limits, which is in the 500–600 Ka age range with the present instrumentation (Shen et al. 2001). The results indicate that the youngest member of *Homo erectus* at this site is >400 Ka and the oldest members from the lower layers are significantly older than 500 Ka.

The ^{230}Th/^{232}Th–^{234}U/^{232}Th-isochron technique permits determining the initial ^{230}Th/^{232}Th ratio. Schwarcz (1989) used this technique for dating the sinter crust on the cranium of the classic Neanderthal at Monte Circeo, central Italy. The encrustation on the cranium consisted of a brighter inner and a dark-brown outer layer. The outer layer provided an age of 16 Ka. From the inner layer, which contained detrital contamination, several subsamples of different U/Th ratios were obtained through fractionated leaching. The slope of the straight line (isochron) through the data points in the ^{230}Th/^{232}Th–^{234}U/^{232}Th diagram provided a more reasonable age of 51 ± 3 Ka.

Precise ^{230}Th/^{234}U dating of *travertine*, a spring sinter built from secondary carbonates, is hampered by the common detrital ^{230}Th-contamination and by open-system behavior. Applying a micro-sampling technique, in which 100 mg of sample material was selectively drilled from the micrite/sparite phases, Mallick and Frank (2002) dated successfully travertines from various Thuringian (Germany) sites, among them Weimar-Ehringsdorf with pre-Neanderthal remains. The results assign these finds firmly to oxygen-isotope stage 9.

Buried *teeth* absorb uranium from the groundwater. The knowledge of the time function of the uranium uptake is crucial for the ^{230}Th/^{234}U-age evaluation. Since the exact temporal development of uptake is unknown, one has to rely on models, such as early (EU) or linear (LU) uptake (cf. ESR), and must also consider leaching. For instance, the age of Neanderthal remains from Payré (France) was constrained by direct LA-MC-ICPMS U-series analysis of a Neanderthal tooth yielding an apparent minimum age of 200 Ka, which is in good agreement with TIMS U-series ages for an underlying flowstone between 200 and 230 Ka (Grün et al. 2008).

The mode of uranium uptake can be constrained when ^{230}Th/^{234}U is combined with ESR dating (Grün et al. 1988; Shao et al. 2012) which now is more common practice than stand-alone U series of organic tissue. With a combination of Th/U and Pa/U dating, it is theoretically possible to obtain ages back to 1 Ma, but analytical constraints limit the potential range to 600–700 Ka, and application is hampered by the required large sample size (Grün et al. 2010). Falguères et al. (1997) reported coupled ^{230}Th/^{234}U and ESR dating on horse teeth from Acheulian and Mousterian levels at la Micoque, France. The ^{230}Th/^{234}U ages of enamel and dentine ranged widely from 150 to $>$350 Ka. However, when combined with ESR dating, consistent ages between 300 and 350 were obtained. Open-system behavior is even more crucial for U-series dating of bones, and the development of new models is essential (Sambridge et al. 2012). Sophisticated techniques and multiple approaches are required to provide ages for bones by U series and preferentially should be supported by independent age evidence. However, this approach can serve as a tool for the verification of the antiquity of bones or determining if bones are intrusive and not of the same age as associated material. This was how the antiquity of one of the earliest modern humans (Omo Kibish 1) was confirmed. Agreement with Ar/Ar dating of 195 Ka for correlated material was obtained by a minimum age of 155–187 Ka with LA-MC-ICPMS U series, on bone fragments believed to belong to the calvaria (Aubert et al. 2012).

In principle, nondestructive U-series dating techniques based on γ-spectrometry can be used on valuable specimens. However, the complex detection geometries of human remains and the low resolution of the method prevent standard application, and uncertainties of results are large, usually preventing the determination of appropriate U-uptake models (e.g., Schwarcz et al. 1998 vs. Millard and Pike 1999).

Fission Track

Although fission tracks (FT) are not applied as commonly as the other radiometric dating methods in paleoanthropology, they have made significant contributions at some important sites in volcanic regions. Fission tracks are formed by the spontaneous nuclear fission of uranium. Natural uranium consists of the isotopes ^{238}U (99.3 %) and ^{235}U (0.7 %), whereby ^{238}U decays by spontaneous fission. The fission decay rate is 10^6 times less than that of the α-decay of the same isotope. During fission the uranium nucleus splits up into two fragments. Due to their kinetic energy, both fission fragments are expelled in opposite directions and leave along their path a zone of damage in the crystal lattice of a mineral. Both branches together form a straight fission track of 10–20 μm in length and several 10^{-3} μm in diameter. By chemical etching, the fission tracks can be made visible for optical microscopy. In the course of time, the tracks accumulate in the mineral, and if they are all preserved, their number is a function of the age of the event dated. Obviously, the track number depends also on the uranium content which is determined by exploiting the thermal-neutron-induced fission of ^{235}U, where the number of the induced ^{235}U fission tracks is proportional to the U content. Thus, the procedure of fission-track dating essentially involves the counting of spontaneous ^{238}U fission tracks before and induced ^{235}U fission tracks after a neutron irradiation.

The principles and application of fission-track dating were described in detail by Wagner and Van den haute (1992). With fission tracks, either the age of mineral formation or its last heating when all previous tracks were erased, i.e., the clock was reset, is dated. The fission-track method is applicable for a time span of >10 Ka. This requires, however, sufficiently high uranium contents above 100 μg g^{-1}. Zircon, due to its high uranium content, is most frequently used in paleoanthropological applications. Of particular interest are volcanic ashes that are intercalated in sedimentary sequences containing hominid remains and Paleolithic sites. Also volcanic glass, such as obsidian and pumice, is frequently used for fission-track dating.

A common problem in fission-track dating is the annealing of tracks. Latent fission tracks gradually fade over time. The fading is accelerated at elevated temperatures, in a process known as annealing. Since annealing reduces the apparent fission-track age, it is of fundamental importance to quantify this effect by track-length measurement, since annealing shortens the tracks. Fortunately, tracks in zircon are rather stable and do not show any signs of fading over several million years at ambient temperatures, although tracks in natural glasses certainly may fade under such conditions.

For fission-track dating of tephra, mainly zircon grains and, to a lesser degree, also glass shards and apatite as well as titanite grains are used. When relying on heavy minerals, the possible different provenance of the various grains needs to be taken into consideration, a difficulty already discussed (cf. K–Ar dating). Primary volcanic grains in the presence of detrital ones can be identified – apart from mineralogical criteria – by single-grain fission-track data. A good case study was conducted for the Pliocene/Pleistocene sedimentary sequence of the Koobi Fora formation, Kenya. It contains several tuff horizons, which primarily consist of glass fragments and pumice cobbles, but shows signs of redeposition. Of particular interest is the KBS Tuff, which is intercalated in hominid-bearing layers. In the 1970s, K–Ar data on the KBS Tuff raised a controversy between supporters of a long chronology (2.61 ± 0.26 Ma: Fitch and Miller 1970) and those of a short chronology (1.82 ± 0.04 Ma; Curtis et al. 1975). FT dating on zircon (2.44 ± 0.08 Ma; Hurford et al. 1976) at first seemed to support the high K–Ar age. A later FT study of zircon from the pumice yielded 1.87 ± 0.04 Ma (Gleadow 1980) in accordance with the short chronology. Besides methodological aspects, the main reasons for the previous fission-track overestimate of the KBS Tuff are detrital, old zircon grains. A far-reaching study on tuffaceous zircon was reported by Morwood et al. (1998). At the site of Mata Menge, Flores (Indonesia), a layer with stone tools is intercalated in tuffaceous deposits. FT dating on zircon from the lower and the upper tuffaceous layer yielded 880 ± 70 Ka and 800 ± 70 Ka, respectively. Provided that these grains are primary and not reworked, these findings imply that at that time *Homo erectus* had already reached the island of Flores from Southeast Asia – a journey that requires an amazing sea-crossing capability, even at periods of lowest sea level.

Ashes in prehistoric fireplaces may contain sufficiently heated grains of apatite, zircon, and titanite. At Zhoukoudian near Peking, with its numerous remains of *Homo erectus* (Peking man), several hundred grains of titanite in the size range of 50–300 μm were separated from ashes sampled from layers 10 and 4. The length of the fission tracks was utilized as criterion for discriminating completely from partially annealed titanite grains. Altogether, 100 grains showed complete resetting and gave mean ages of 462 ± 45 Ka for layer 10 and 306 ± 56 Ka for layer 4 (Guo et al. 1991), which are younger than the abovementioned uranium-series ages for this site (Shen et al. 2001).

Luminescence

Since its introduction by Daniels et al. (1953), luminescence dating has gradually developed into a powerful chronometric technique, particularly for quartz- and feldspar-bearing materials (Aitken 1985, 1998; Bøtter-Jensen et al. 2003; Yukihara and McKeever 2011). In the meantime, luminescence dating has significantly contributed to paleoanthropology. As to the techniques of luminescence dating, one distinguishes between thermoluminescence (TL) and optically stimulated luminescence (OSL). For the latter the term “optical dating” is also used. Luminescence dating covers a wide age range between 10 and 10^5 years and thus is able to reach well beyond the limits of radiocarbon dating. Datable materials comprise various inorganic sediments, such as sand and loess, heated stones, and bleached stone surfaces.

Luminescence dating is based on the time-dependent deposition of energy in the crystal lattice of minerals. This energy stems from ionizing radiation, which originates from natural radioactivity, as well as cosmic radiation and is omnipresent in nature. The radiation, consisting of energetic α- and β-particles as well as photons (γ-rays), interacts with the atoms of a mineral and removes some electrons from their original valence-band position in the atom shell. Freed electrons diffuse for a short distance through the crystal lattice, and some of them become trapped in lattice imperfections. Such electrons are trapped at higher energetic levels than those in the valence band. With time t the electron traps are increasingly filled – the process that forms the basis of the luminescence clock. When the crystal is stimulated by heat or light, the electrons are released from their traps, enabling them to recombine with opposite charge carriers whereby the formerly trapped energy is set free. Some of this energy appears as emission of visible light, the luminescence. Depending on the kind of stimulation, one differentiates thermally (TL) from optically stimulated luminescence (OSL) from radiofluorescence (RF), the latter of which is stimulated by ionizing radiation. OSL is further differentiated according to the type of stimulating light, such as OSL by green/blue or IR-OSL (IRSL) by infrared stimulation. Recent approaches consist of various steps of heating and illuminating the samples (e.g., post-IR IRSL) or employ the isothermal decay of the luminescence signal (IT-TL) for dating.

The intensity of the luminescence signal is related to the accumulated energy dose *AD* (in unit of Gray, *Gy*) and, thus, to the time interval *t* (age) during which the mineral has been exposed to the ambient ionizing radiation. The luminescence age is calculated from the accumulated *AD* and the rate of ionizing radiation *DR* (dose per time, in unit of $Gy\ a^{-1}$).

$$t = AD/DR \tag{7}$$

From this equation, it becomes clear that the dating procedure consists of two steps: the determination of *AD* and *DR*.

With increasing radiation dose, the number of empty traps still available becomes fewer, so that the growth curve of the luminescence signal assumes the shape of exponential *saturation*. In most cases saturation is reached after doses of few 10^2 Gy. This behavior restricts luminescence dating to the last few 10^5 years. In order to convert the luminescence signal into a dose value (*AD*), the *sensitivity S* to ionizing radiation (luminescence signal per dose, i.e., the slope of the growth curve) has to be determined, varying from sample to sample. For a given sample, it is the same for β- and γ-radiation but different for α-radiation. The sensitivity ratio S_α/S_β, the so-called a-value, needs to be determined, but is mostly around 0.1.

Another behavior limiting the age range is *fading* of the latent luminescence signal in the course of time, violating the prerequisite that all centers involved in the signal generation are stable over the complete age range in question. Like any other type of radiation damage, latent luminescence signals are subjected to fading whose kinetics is essentially thermally controlled. As far as near-surface materials at normal ambient temperatures are concerned, natural fading limits the datable age range up to a few 10^5 years.

An important concept in dating is the *resetting* of the system: The luminescence systems need to have been reset at the event of interest. Complete or at least partial resetting of the latent luminescence signals is caused by exposure to heat or light. Consequently, the last occurrence of such an event can be dated, for example, the deposition of sediments or the heating of flint artifacts.

The past few years have seen a lot of progress in laboratory protocols. Previously, it was common practice in *AD* evaluation to prepare multiple subsamples (aliquots) and apply various doses in addition to the natural one. Lately, the so-called SAR protocol (Single Aliquot Regeneration) is increasingly preferred, which regenerates the luminescence signal after artificial resetting (Murray and Wintle 2000).

When using regenerated growth curves, *AD* is evaluated through the value of the artificial dose required to produce exactly the same luminescence intensity as the natural one. In order to normalize for sensitivity changes due to the laboratory procedure, a constant test dose is applied and measured for each aliquot at every step in the procedure. However, it is debated if the initial sensitivity changes can be accounted for (e.g., Singhvi et al. 2011). The advantages of the SAR protocol over the conventional multiple-aliquot (MA) technique are smaller sample size, less time for sample preparation, and improved analytical precision due to replicate *AD* determination. The present technology is directed towards single-grain protocols that allow the differentiation of *AD* populations in order to select the results from grains showing the same apparent luminescence age on statistical grounds, which bears a great potential for novel applications (Roberts et al. 1997; Greilich et al. 2002; Greilich and Wagner 2006; Jacobs et al. 2003, 2013).

Apart from the accumulated dose *AD*, the natural dose rate *DR* needs to be determined for the age calculation. The ionizing radiation at the Earth's surface originates predominantly from the radionuclides ^{232}Th, ^{235}U,^{238}U, and their daughter products, as well as ^{40}K and ^{87}Rb and, to a minor extent, from cosmic rays. These nuclides emit α-, β-, and γ-radiation, each of which has a different penetration depth, amounting in rocks to ca. 20 μm, 2 mm, and 30 cm, respectively. The internal component originating within the luminescence sample as well as the external radiation from the immediate surroundings, i.e., sediment, has to be taken into account. The age determination requires materials of a uniform and defined dose rate. For this reason one separates the sample into certain sizes, usually the fine-grain (4–10 μm) or coarse-grain (100–200 μm) fractions. Since any water residing in pore volumes attenuates the dose rate, the moisture content and its possible temporal variation in the sample as well as its environment need to be estimated. Also the on-site intensity of the cosmic rays has to be assessed. It mainly increases with topographic altitude and decreases with depth below the surface. Temporal variation of the dose rate might be caused by changing contents of radionuclides in sediment due to disequilibrium within the decay chains. All these factors have to be considered carefully, since they may cause major uncertainties in luminescence dating. For dose-rate evaluation, several techniques are available, among them α- and β-counting, γ-spectrometry, atomic absorption, ICP-MS, and neutron activation analysis.

Luminescence dating of *clastic sediment* enables to determine when it was deposited, provided all of the sedimentary grains were sufficiently exposed to daylight before and during deposition. In this way paleoanthropological remains which are embedded in such sediment series can be dated. In Central Europe – as well as in other periglacial areas – numerous loess profiles with Paleolithic finds have been TL dated (e.g., Zöller et al. 1991). Also many sands have been dated by OSL. An example is the dune sands of the Acheulian open-air site of Holon/Israel where alkali feldspar and quartz fractions were dated by OSL as well as TL (Porat et al. 1999). The presence of sediment remnants in the endocranial cavity of a modern human from Hofmeyer (South Africa) allowed the OSL dating of the deposition of the skull, despite the impossibility of locating the original position of the specimen in its sedimentological context. Quartz grains were extracted and yielded OSL ages of 40.9 ± 4.2 Ka, 33.0 ± 2.5 Ka, and 34.7 ± 3.4 Ka, which were combined to a depositional age of the endocranial sediment of 36.2 ± 3.3 Ka (Grine et al. 2007).

However, the presumption that all grains had been completely bleached at deposition is not necessarily fulfilled. In particular, fluvial sands, where grains were transported under water cover, may contain partially bleached or even unbleached grains. In this case the apparent luminescence age would be an overestimate. Also, post-depositional vertical mixing between sedimentary layers, such as bioturbation, leads to erroneous ages. In addition to such phenomena, trampling and human modifications might lead to sediment particles being displaced in archaeological sites.

Luminescence measurements of individual grains enable the identification of such disturbances. Because of microdosimetric concerns, this might not always be straightforward because a priori it cannot be differentiated whether the determined *AD*s are influenced by bleaching or the heterogeneity of the radiation field (microdosimetry). Single-grain OSL dating is always based on the interpretation of statistical analysis of *AD* results. Strictly, the models applied are those for dose, and not “age” models, which are always analyzed under the assumption of the validity of the statistical parameters and models employed. The potential of single-grain OSL dating was convincingly demonstrated in the case of the Jinmium rock shelter in northern Australia. Fullagar et al. (1996) reported TL ages of 176 ± 16 Ka and 116 ± 12 Ka for the artifact-bearing deposit, which would predate other results for the first arrival of humans in Australia by more than 100 Ka. The data were determined on multiple-grain aliquots of quartz, despite the known presence of erosional fragments from the mother rock in this sandstone abri. An intensive OSL-dating program on the same deposits by Roberts et al. (1999), using the single-grain approach, yielded ages of less than 10 Ka when considering only those grains which had been fully bleached before burial. Furthermore, in Australia single-grain OSL ages of quartz from Malakunanja II now date the early human occupation to 55.5 ± 8.2 Ka (Roberts et al. 1998) and the human burials of Lake Mungo to 40 ± 2 Ka (Olley et al. 2006).

Burned flint is well suited for TL dating. Due to a relatively low internal dose rate and good TL-stability behavior, its datable age range reaches back to at least 500 Ka and thus covers a large part of the Paleolithic period. TL dating of flint requires prehistorical annealing (>400 °C) of the TL signal, which, fortunately, has been the case for a considerable number of flint artifacts. Because of the dosimetric heterogeneity of most archaeological sites, it is advisable to collect several flint samples from each layer to be dated. Heterogeneity of the internal dose rate can be suspected for flint or similar materials. Such heterogeneities were shown by autoradiography for some samples (Schmidt et al. 2013), but were significant for dose evaluation only in macroscopically well-visible inclusions or veins. Such samples are usually rejected from analysis in any case, because of suspicions of differences in mineralogy and thus luminescence properties, unless mineral phases can be separated. Most TL-dating applications of burnt flint follow MA protocols, which require individual sample sizes larger than can be provided from many sites where burnt material is scarce and small. Detecting the luminescence in a different wavelength, however, allows the successful application of the SAR protocol and thus on small sample sizes (Richter and Krbetschek 2006). Perfect agreement with independent other dating evidence is obtained for an Eemian age site, allowing the direct dating of a prehistoric human activity (Richter and Krbetschek 2014; Sier et al. 2011).

Intensive TL-dating studies were carried out at several Levantine sites with rich Lower to Middle Paleolithic lithic industries and human remains of Neanderthals as well as early Moderns. From the site of Tabūn/Israel, Mercier and Valladas (2003) report stratigraphically consistent TL ages between 302 ± 27 Ka and 165 ± 16 Ka, indicating that the technological transition from the Acheulian to the Mousterian occurred some 250 Ka ago. Thermoluminescence dating of heated flint revealed the antiquity of the North African technocomplex of the Aterian and its problematic use as a chronostratigraphical meaningful unit. The TL dating of a stratigraphical succession of alternating Aterian (AT) and Mousterian (MOU) industries at Ifri n'Ammar (Morocco) resulted in 83.3 ± 5.6 Ka (AT), 130.0 ± 7.8 Ka (MOU), 145 ± 9 Ka (AT), and 171 ± 12 Ka (MOU) in correct stratigraphic order (Richter et al. 2010).

At the site of Kebara (Israel), a skeleton of a Neanderthal and, at the sites of Qafzeh and Skhūl, remains of archaic early modern humans were recovered. TL dating on 20 flint fragments from the hominid-containing layer in Qafzeh yielded 92 ± 5 Ka. At Kebara, 30 flint artifacts from several layers provided TL ages from 50 to 70 Ka, and the layer with the skeleton of the Neanderthal provided 60 Ka. At Skhūl six burnt flints from the level with the remains of archaic early modern humans yielded a TL age of 119 ± 18 Ka (Mercier et al. 1993). These data reveal that early forms of anatomically modern humans were present in the same geographical area as Neanderthals long before modern humans spread into Europe. However, these findings do not reveal if both species were occupying this area at the same time and an alternating scenario related to climate changes is favored.

At the early Upper Paleolithic site of Geißenklösterle/Germany, seven flint artifacts from the Early Aurignacian, and two from the Aurignacian levels, ultimately satisfied the criteria of being sufficiently heated (Richter et al. 2000), providing weighted mean ages of 40.2 ± 1.5 Ka and 37.0 ± 1.4 Ka, respectively. The disagreement with radiocarbon ages on bones from the same levels was later determined to have been caused by insufficient removal of contaminants in radiocarbon dating (Higham et al. 2012). The radiocarbon ages confirm the TL data and show their accuracy, while altogether these data imply a much earlier beginning of the Upper Paleolithic figurative art in Central Europe than anywhere in Western and Southwestern Europe.

A novel development is the OSL dating of stone surfaces, when daylight exposure in the past reset the OSL signal. Provided the surface was shielded from light since then, the moment of the last exposure to daylight can be determined. This approach opens – at least in principle – a large potential for archaeological, paleoanthropological, and geomorphological applications such as the dating of the construction and destruction of stone structures and buried lithic implements as well as deposited boulders. Hitherto, the new method has been corroborated for

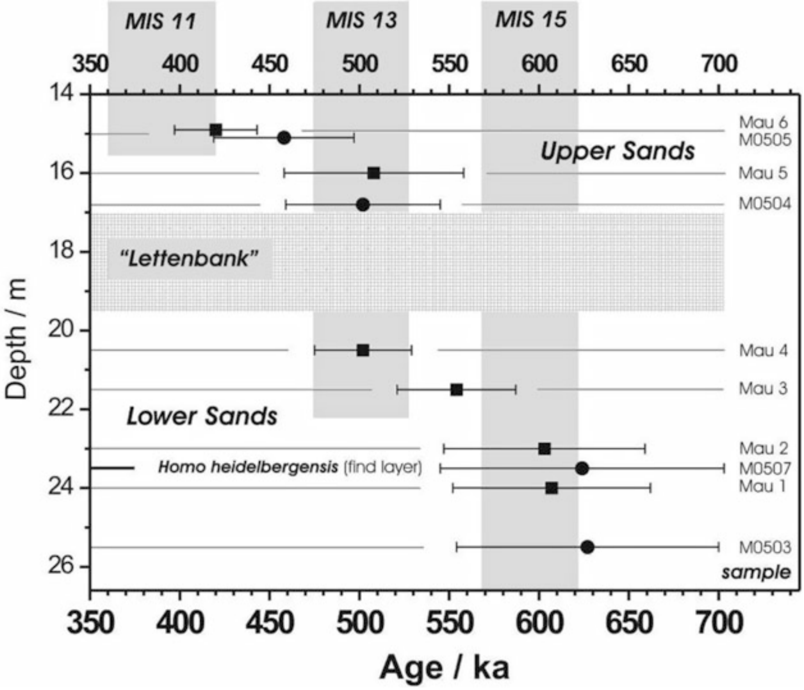

Fig. 2 IR-RF (*squares*) and ESR/U-series (*circles*) ages with 1-σ uncertainties of samples from the sand pit Grafenrain at Mauer (From Wagner et al. 2010)

granitoid rocks and successfully applied in particular to the famous Nazca geoglyphs in southern Peru (Greilich et al. 2005; Greilich and Wagner 2006).

Infrared radiofluorescence (IR-RF) is a new method developed by Trautmann et al. (1998) for potassium feldspar and is of particular interest for age ranges beyond 10^5 years because of its long-term signal stability (Erfurt and Krbetschek 2003). This new method has been shown to provide excellent agreement with a large number of independent age estimates (Degering and Krbetschek 2007). For example, IR-RF dating of the "Mauer sands" at the holotype site of *Homo heidelbergensis* is in excellent agreement with electron spin resonance dating of animal teeth from the sequence (Fig. 2). However, concerns have been raised on the general applicability (Buylaert et al. 2012), and more data from more than the currently only two laboratories is needed.

Various other new luminescence techniques are applied to establish the time of bleaching of sedimentary deposits. Namely, thermally transferred optical stimulation (TT-OSL) and post-infrared infrared stimulated luminescence (post IR-IRSL or pIRIR) are more frequently applied, including sites of paleoanthropological interest (e.g., Sun et al. 2013; Schmidt et al. 2011, respectively). The accuracy of such recent developments, however, has not been shown by fully independent methods so far.

Electron Spin Resonance

Electron spin resonance (ESR) dating is also based on the accumulation of radiation-induced energy in minerals and thus has close links to luminescence dating. Although first attempts to exploit the ESR phenomenon for dating go back to the 1960s (Zeller et al. 1967), it did not flourish as a dating method before the 1980s and is still being developed. The ESR method permits age determination up to a few million years, far beyond the range of the luminescence methods, and covers the whole Quaternary period. The most important material for paleoanthropological application is tooth enamel, but quartz separates from sediments at prehistoric sites also have a certain potential (Rink 1997), as well as fluvial sediments. With ESR dating, either the event of the death of a mammal (set equal to sediment deposition and/or, e.g., human occupation), the resetting of a previous system as a result of bleaching of sedimentary quartz grains, or the event of heating of stones is dated.

The ESR phenomenon is caused by paramagnetic centers in the crystal lattice. Radiation-induced trapped electrons (see "Luminescence") form such centers and give rise to characteristic ESR signals. The intensity of the ESR signal is a function of the number of trapped electrons and therefore of the accumulated energy dose *AD* that has been absorbed from the ionizing radiation in the course of time. In order to calculate the ESR age, the value of *AD*, obtained from the ESR measurement, is divided by the dose rate *DR*, in the same manner as already discussed for luminescence (Eq. 7).

The quantity of *AD* is determined by ESR spectrometry, which exploits the fact that trapped electrons are unpaired. Brought into a variable magnetic field and exposed to a given microwave, unpaired electrons show spin resonance at a specific strength of the magnetic field. The condition at which resonance happens is described by the g-value, which is characteristic for the type of the paramagnetic center. The energy necessary for the resonance is absorbed from the microwave so that its intensity reduction is a measure for the concentration of the center. The resulting ESR spectrum shows the specific microwave absorption for various centers with different g-values. Owing to measurement-technical reasons, the ESR spectra of the microwave absorption are not directly recorded; instead their first derivation as a function of the field strength is plotted. For the evaluation of *AD*, known artificial doses are applied in addition to the natural one and a signal growth curve is established. ESR has the advantage over luminescence that the concentration of the probed centers is not disturbed by the measurement procedure, thus permitting one to establish an additive growth curve with accumulating doses on the same aliquot. Most samples show exponential saturation functions. At normal ambient temperature of sediment, most ESR centers are sufficiently stable for applying ESR dating up to a few million years. The dose-rate determination follows the same principles as already mentioned for luminescence. For ESR-dating samples of a few grams are sufficient, provided the material is homogenous, but usually larger sample sizes are preferred as they allow the separation of suitable materials in the laboratory to conduct microdosimetric measurements.

ESR dating of fossil *tooth enamel* plays an important role for Paleolithic sites, mainly because teeth are commonly preserved. Mammalian dental issue consists essentially of enamel, dentine, and cementum layers. ESR dating is based on the mineral hydroxyapatite, in particular on its carbonate-containing subspecies dahllite, within the enamel. Dentin and cementum are less dense, contain more organic tissue, and take up uranium more easily than enamel. For these reasons, they are not used for ESR analysis, but must be taken into account for microdosimetric reasons. The ESR spectrum of tooth enamel has, at $g = 2.0018$, a suitable signal of good sensitivity and high thermal stability.

The quantity of the dose rate introduces considerable problems into ESR-age evaluation. Strongly varying uranium contents on the microscopic scale often cause steep dose-rate gradients in teeth, which is in particular the case for the β-component since the β-radiation range (ca. 2 mm) is similar to the thickness of the enamel layers. Teeth gradually take up uranium from the groundwater after burial. In vivo they contain less than 1 $\mu g\ g^{-1}$ of U, but fossil ones have up to 1,500 $\mu g\ g^{-1}$. This means that the dose rate increases with time and that the closed-system condition is not fulfilled. To allow for the time dependence of the dose rate, distinct models of uranium uptake are assumed, such as the early uptake (EU), the linear uptake (LU), and recent uptake (RU) models. The EU model results in a lower ESR age compared to the LU model due to a higher dose rate on the average. Both model ages may considerably differ from each other, especially for sample with high uranium contents so that samples low in uranium are preferable. Most published ESR-age data are based on assumed U-uptake models. In order to set constraints to the validity of the model, ESR dating is coupled with uranium-series dating (Grün et al. 1988), with new uptake models developed by Shao et al. (2012). The comparison of theoretical closed-system ages of $^{234}U/^{238}U$ and $^{230Th}/^{234}U$ with that of ESR enables to discriminate among the hypothetical models. Combined ESR/uranium-series dating has become more and more the routine for tooth enamel dating.

The Early and Middle Paleolithic sites of Tabūn, Kebara, Skhūl, Qafzeh, and Hayonim (Israel), with rich lithic and human bone inventories, play a fundamental role with respect to the early human out-of-Africa dispersion through the Levantine corridor. In order to establish a firm chronology of this process, ESR dating has been repeatedly applied to mammalian tooth enamel from these sites, in addition to uranium series and luminescence. Worth mentioning in this context are two results in particular. First, the combined ESR/uranium-series tooth age of 387 ± 50 Ka confirms a 340 ± 33 Ka TL age on burnt flint for the Lower Paleolithic Yabrudian lithic industry at Tabun, whereby the U uptake appears to be more recent than linear (Rink et al. 2004). Second, the ESR ages on teeth from Middle Paleolithic contexts support the early dating of anatomical Moderns to 80–120 Ka, with the amazing consequence that the Levant was alternating, inhabited by Moderns and Neanderthals for about 60 Ka.

At the well-known South-African site of Swartkrans, with its wealth of remains of *Australopithecus robustus*, Curnoe et al. (2001) determined one of the oldest ESR ages so far reported. Coupled ESR/uranium-series dating on two human and two bovid teeth yielded 1630 ± 160 Ka, with a possible maximum of 2110 ± 210 Ka, indicating that ESR dating can provide reasonable results for samples of Late Pleistocene/Early Pleistocene age. Also the Atapuerca Gran Dolina site, northern Spain, with the earliest human remains in Europe of *Homo antecessor*, was investigated by combined ESR/uranium-series dating. From the bottom of the Aurora stratum, where the very early human remains were recovered, three ungulate teeth gave a mean age of 731 ± 63 Ka, which is in agreement with the paleomagnetic age estimate of >780 Ka (Falguères et al. 1999).

ESR also permits the dating of calcareous sinter deposits that show complex ESR spectra partially as a result of organic radicals. Important Paleolithic cave sites have been dated, among them Caune de l'Arago at Tautavel, southern France. ESR dating of calcareous deposits under- and overlying the hominid-bearing layer allowed its bracketing between 242 and 313 Ka as upper and 147 Ka as lower age limits, respectively. This result is in good agreement with uranium-series data of 315–220 Ka (Hennig and Grün 1983).

The holotype of *Homo heidelbergensis* was found in 1907 in fluvial sands at Mauer near Heidelberg. The associated mammalian fauna and the geological context place the find layer in the early Middle Pleistocene, but confirmatory chronometric evidence has only been recently achieved by the coupled ESR/U-series dating of mammal teeth and infrared-radiofluorescence dating (IR-RF) of feldspar grains from the sands (Wagner et al. 2010). These "Mauer sands" are subdivided into two distinct units, the "lower sands" and the "upper sands," separated by a clay/silt layer (Fig. 2). The mandible of *Homo heidelbergensis* was recovered from a 0.1 m thick gravel layer within the "lower sands." Both sand units are renowned for their rich early Middle Pleistocene mammal faunas, which clearly indicate warm climate conditions. The good preservation of the mammal bones – and in particular of the human mandible – indicates that they were transported from a nearby fluvial floodplain before becoming embedded in the river deposits, i.e., they have the same geological age as their surrounding sediment layers. Eight herbivore teeth (five from the "lower sands" and three from the "upper sands") were analyzed with the ESR/U-series technique. Most of the Mauer dental-tissue samples show evidence of postmortem uranium uptake, allowing the calculation of reliable ages (Fig. 2). The IR-RF ages determine the last light exposure of sand grains, i.e., their depositional age. Ten samples from six sediment layers of both sand units were dated using small subsamples of K-feldspar grains (Fig. 2). The weighted mean of the two sand samples Mau 1 and Mau 2, and the dentine sample M0507, yields 609 ± 40 Ka for the find layer of *Homo heidelbergensis*. This result demonstrates that the mandible is the oldest hominin fossil reported so far from Central and Northern Europe.

ESR may also be applied to quartz grains from *clastic sediments*, provided the grains were exposed to light for about 6 months during sedimentary transportation so that the minimum signal level in Al centers is reached. However, there are so far only a few examples of successful application in paleoanthropology, one being the early Pleistocene Monte Pogglio site, Italy, where more than 4,000 Paleolithic flint artifacts were found in sandy beach deposits. Detrital quartz extracted from different archaeological levels provided a mean age of 1065 ± 165 Ka, which is in agreement with paleomagnetical data (Falguères 2003).

Radiocarbon (^{14}C)

Among the physical dating methods, radiocarbon is the most widely known and most commonly applied in archaeology. Essentially, it utilizes organic remains from the last 50 Ka. In the context of paleoanthropology, this covers only the periods from the Late Middle Paleolithic onwards, which comprise a relatively short section of human presence on Earth. Furthermore, its application in the pre-Holocene time range (>12 Ka) is complicated by the fact that calibration procedures for ^{14}C dates cannot be based on high-precision tree-ring data, resulting in low accuracy of the true age. Towards the upper age limit, contamination by modern carbon becomes a dominating problem.

Recent natural carbon consists of the two stable isotopes ^{12}C (98.89 %) and ^{13}C (1.11 %), and in very minor traces the radioactive ^{14}C ($^{14}C/^{12}C \times 10^{-12}$) that decays ($t_{1/2} = 5730$ a) under β-emission. ^{14}C is naturally produced in the stratosphere by interaction of neutrons from cosmic rays with atmospheric nitrogen atoms according to the reaction ^{14} N(n,p)^{14}C. The average global ^{14}C production rate is 7.5 kg a^{-1}, but is subject to considerable temporal variation. Depending on this rate, an equilibrium value between production and radioactive decay is established. Bound in CO_2, ^{14}C becomes quickly distributed throughout the atmosphere. By photosynthesis CO_2 enters the plants and via the food chain the biosphere. Through dissolution and gas exchange, it is introduced into the hydrosphere, from where it is incorporated as $CaCO_3$ into marine or limnic sediments and organisms. As long as these reservoirs participate in the carbon cycle, their ^{14}C concentration maintains the atmospheric equilibrium value.

The carbon becomes separated from the cycle with the death of the organism or with carbonate precipitation, so that the ^{14}C input is interrupted. Thereupon, the $^{14}C/^{12}C$ ratio declines due to the radioactive decay of ^{14}C. Initially it was assumed by Libby (1952) that the atmospheric $^{14}C/^{12}C$ was constant. According to this model, the *conventional* ^{14}C age is calculated (cf. Eq. 5) from the present $^{14}C/^{12}C$ and an assumed fixed value for $(^{14}C/^{12}C)_0$. The conventional ^{14}C age is linked to the reference year 1950 AD, with the notation "BP" (before present).

Conventional ^{14}C ages do not directly provide the right age information, since the simple model condition of a constant initial $^{14}C/^{12}C$ is invalid. Tree-ring data, for instance, show that within the past 11 Ka, the initial $^{14}C/^{12}C$ decreased by ca. 10 %, so that a 10 Ka old sample results in a ^{14}C age being ca. 1 Ka too young. In order to obtain accurate ages, the temporal fluctuation of ^{14}C must be corrected for. This is achieved by ^{14}C dating of samples of independently known age (e.g., tree rings). Apart from possible oscillations of the primary cosmic ray flux, the fluctuations in the atmospheric $^{14}C/^{12}C$ level are attributed to changes in the ^{14}C-production rate, caused by the varying magnetic shielding of the primary cosmic rays; in particular the geomagnetic minimum ca. 40 Ka ago doubled the production rate (Beck et al. 2001). Also, magnetic disturbance originating from solar activity modifies the production rate, although to a lesser degree and on shorter time scales. In this way, high magnetic intensities imply low ^{14}C-production rates and, thus, high apparent ^{14}C ages. On the other hand, the carbon exchange between different reservoirs, mainly the ocean and the atmosphere, affects the atmospheric $^{14}C/^{12}C$ level. In periods, when the oceanic circulation slows down, less of the "aged" oceanic CO_2 is released into the atmosphere, so that atmospheric $^{14}C/^{12}C$ level increases, leading to apparently younger ^{14}C ages.

Regardless of their origin, these fluctuations necessitate calibration of the ^{14}C results. By calibration the chronologically irrelevant *conventional* radiocarbon age is converted to a calendar time scale. This is achieved via calibration curves, in which conventional ^{14}C ages are plotted versus the true known calendar ages of the same samples determined by other means. For the Holocene this is achieved with high accuracy by dendro-calibration. For the late Pleistocene, other archives than tree rings are needed due to the scarcity of trees during glacial climate. Annually varved sediments, shallow-water corals, and planktonic foraminifera, which can be independently dated with uranium-series techniques, have been used for this purpose, with the latest efforts presented as the INTCAL09 curve (Reimer et al. 2009). While this calibration curve covers the entire radiocarbon age range of ca. 50 Ka, its reliance on marine material for the correction of terrestrial material is not favorable because of the required marine reservoir correction. However, the IntCal13 radiocarbon calibration curve under construction will be much more based on terrestrial high-precision records of the varved sediments from Lake Suigetsu (Bronk Ramsey et al. 2012) in its lower age range, together with speleothems from the Bahamas and Hulu Cave, and support from marine data for its entire time range (Reimer et al. 2013).

Nevertheless, a particular complication resulting in lower precision is posed by the strong ^{14}C fluctuations that are associated with the magnetic minima during the Laschamp and Mono Lake geomagnetic excursions around 40 and 33 Ka ago, respectively, which are crucial periods in the peopling of Europe.

In order to distinguish calibrated ^{14}C ages from conventional ones, they are characterized by the notations "cal BC" (calendar years BC), "cal AD" (calendar years AD), or "cal BP" (calendar years before 1950 AD). In publications it always has to be stated which calibration curve and which software were used. Furthermore, the original radiocarbon date should always be provided together with the lab code. This will allow future calibration with improved calibration curves that are expected to provide increased precision and accuracy, as has already been the case for the dendro-calibrated age range.

Apart from the temporal fluctuations, problems arise from spatial ^{14}C inhomogeneities in the materials and reservoirs participating in the carbon cycle. One distinguishes *isotope fractionation* and *reservoir effects*. Photosynthesis, for instance, enriches the light ^{12}C over the heavy ^{13}C, and in turn the latter over the even heavier ^{14}C, so that the carbon in plants is isotopically lighter than in the atmosphere. For most materials, the age corrections caused by isotope fractionation are less than 80 Ka, but may amount up to several hundred years, as in the case of marine limestones and organisms. The *reservoir effect* deals with the isotopic variation of carbon within the reservoir, from which the organisms extract their carbon. Such spatial changes may have various causes. If the carbon stays long – with respect to the ^{14}C half-life – within the same reservoir, the ^{14}C concentration declines ("aging" of carbon). A prominent example is the "marine reservoir effect" in the oceans where upwelling regions have present-day apparent ^{14}C ages of around 400 Ka. Also the admixture of "aged" carbon lowers the ^{14}C concentration, such as in the "hard-water effect" in carbonaceous groundwater and surface water. Reservoir effects result in an apparent increase of the ^{14}C age and are difficult to assess.

As in other radiometric dating methods, the ^{14}C system has to remain closed, i.e., carbon must neither enter nor leave the sample. The ^{14}C age is lowered by uptake of recent carbon. Common sources of contamination with recent carbon are the presence of rootlets, humic acid infiltration, and bioturbation. The smaller the authigenic ^{14}C amount and the older the sample is, the more the danger of contamination by modern carbon increases. For this reason the applicability of ^{14}C dating at old ages is limited by unavoidable contamination rather than by the instrumental capabilities of ^{14}C detection. The upper dating limit (*maximum age*) is reached when the ^{14}C of an old sample cannot be discriminated with sufficient statistical confidence from the background. The AMS technique has the great potential to lower the instrumental background and thus to extend the maximum age, but the latter is effectively limited by the ^{14}C background due to contamination of samples themselves and by sample preparation, as well as by techniques employed for sample purification. As a rule of thumb, the oldest radiocarbon age from a given context with unequivocal association with the sample and that satisfies all quality criteria would provide the closest radiocarbon age estimate of the true age where contamination of samples is believed to be a problem. Recent developments in pretreatment chemistry to remove contamination have yielded older radiocarbon age estimates for the majority of samples, but not all.

The amount of sample required for ^{14}C dating depends on the carbon content, the conditions of preservation, the degree of contamination, and the technique of ^{14}C detection. For β-counting, either in gas or liquid scintillation counters, 5–10 g of extracted carbon usually is needed. The AMS technique requires carbon in the mg range. Note that the quoted amounts refer to carbon, and not to sample. The required amount of the latter one might be larger by a factor of 10 or so, depending on the carbon content.

Bones and *antler* are among the most frequently used paleoanthropological sample materials for ^{14}C dating. As long as their inorganic fraction was used, bones were considered as a problematic material for ^{14}C dating due to open-system behavior. However, their organic substance consisting predominantly of various proteins, generally classed as collagen, is more resistant to exchange. The collagen is chemically extracted as acid-insoluble residue, sometimes physically separated (e.g., ultrafiltration), and then usually subjected to AMS analysis. Contamination issues appear to be drastically reduced with procedures like ultrafiltration, but cannot be entirely ruled out a priori, especially for old bones with little collagen preservation or which had been subjected to preservation, e.g., with glue. This is particularly problematic with human bones, which are more frequently treated, and establishing the time of Neanderthal replacement by modern humans has been especially hampered by significantly varying radiocarbon dating results for the same human bones both between and within laboratories. However, by extraction, identification, and subsequent single amino acid radiocarbon dating of the collagen specific compound of hydroxyproline, it can be assured that only carbon from collagen of a particular bone is dated (Marom et al. 2012) and contamination is thus reduced to the maximum extent possible. This specific technique was applied to the early modern human skeleton from Kostenki 14 (Markina Gora), which has been attributed to the Upper Paleolithic but yielded direct radiocarbon ages between 4 and 14 Ka ^{14}C. By single amino acid radiocarbon dating, an age of 33 Ka ^{14}C was established and the Upper Paleolithic age confirmed (Marom et al. 2012).

Such diversities in radiocarbon dating results have fed extended debates particularly on the Neanderthal replacement, which corresponds to the Middle to Upper Paleolithic "transition" of European lithic industries. Human remains are exceptional, and radiocarbon dating of archaeological layers is therefore usually based on associated animal bones, which provided AMS radiocarbon results, e.g., between 28 and 40 Ka ^{14}C for the Aurignacian levels of the Geißenklösterle Cave (Germany). This long time span, which is inconceivable with other evidence, was attributed to unusually strong variations in the production of atmospheric radiocarbon and/or taphonomic processes resulting in the mixing of the bones of various ages within the site. Only a systematic study with thorough decontamination (ultrafiltration) techniques eventually yielded consistent radiocarbon dating results for the site (Higham et al. 2012). The preexisting chronostratigraphy already established by thermoluminescence (TL) dating results on burnt flint (Richter et al. 2000) was confirmed by good agreement. These data show the presence of the Aurignacian and elaborate figurative art earlier than anywhere else in Europe.

Within the same framework, radiocarbon dating of bone has shown the human burial at the Vogelherd Cave (Germany), believed to be associated with similar artwork, to be a Holocene intrusion (Conard et al. 2004). Similarly, a number of other supposedly Upper Paleolithic human remains from Europe were dated by radiocarbon to be of much younger age, emphasizing the crucial requirement of establishing an unequivocal association of dated sample and archaeological context. In light of the recent possibility of single amino acid radiocarbon dating, however, reinvestigations might need to be considered. On the other hand, the oldest directly dated anatomically modern human remains from Peştera Cu Oase (Romania) are not associated with any archaeological remains and are dated by radiocarbon to 34,000–36,000 ^{14}C years BP (Trinkaus et al. 2003), which translates to ca. 42–37.8 Ka cal BP.

Another important dating material is *charcoal*, which is often viewed as much more reliable than bone radiocarbon dating because of more efficient methods for decontamination. In the age range of interest in paleoanthropology, which is close to the limits of the method, however, the application of pretreatment methods indicates underestimation of many radiocarbon dates on charcoal in the 40 Ka range. Comparison of radiocarbon dating of charcoal associated with the independently well-dated Campanian Ignimbrite (CI) tephra showed consistent older and more accurate ages with ABOx-SC pretreatments, compared to the simpler chemical sample preparation of ABA (Wood et al. 2012). Charcoal radiocarbon dating shows the contemporaneity of the lithic technocomplexes of the Proto-Aurignacian and the Uluzzian, the latter of which is considered as a "transitional" industry. While the former is believed to be associated with modern humans, the latter is traditionally assigned to Neanderthals, and these species appear to have occupied different parts of Italy at the same time before the Campanian Eruption 39 Ka ago. Likewise bone radiocarbon dating, the association of charcoal samples should be shown first, e.g., by verification, if the plant species is in accordance with the paleoenvironmental setting.

Limnic sediments form an important archive for the climatic fluctuations of the past, and if they contain organic matter, ^{14}C dating can be directly applied, in particular to peat and sapropel. An excellent material for AMS ^{14}C dating is macrofossils, such as nutshells, fruit kernels, and leaves, recovered from sediments. Such fossils are short-lived and free of the hard-water effect. When dating secondary *calcareous sinter*, the uptake of a certain fraction of "dead" carbon from geologically old limestone must be taken into account, which lowers the reliability of such dates. When using mollusk shells, the marine or hard-water reservoir effect, depending on the habitat of the mollusks, needs to be considered. Paleolithic *rock paintings* commonly contain organic material, such as charcoal, carbonized plant matter, pigments, plant fibers, blood, fatty acids, and beeswax, which enables ^{14}C dating. Radiocarbon dating of micro-samples of charcoal from elaborate rock paintings at the cave of Chauvet-Pont-d'Arc (France), which was sealed by 21 Ka ago, provides further evidence on the early "artistic" expressions of modern humans, with radiocarbon ages around 30 Ka ^{14}C (Valladas et al. 2005). These thus belong among the earliest examples of prehistoric rock art so far discovered.

Cosmogenic ^{26}Al/^{10}Be

The Earth is exposed to a steady flux of cosmic rays – mainly hydrogen and helium nuclei – which interact with the atoms of the atmosphere and reach the Earth's surface strongly attenuated and modified. There they are shortly stopped by nuclear reactions producing in situ radioactive as well as stable cosmogenic nuclei. For dating applications, the radioactive cosmogenic nuclides ^{10}Be, ^{26}Al, ^{32}Si, ^{36}Cl, and ^{41}Ca are used. Due to nuclear reactions, the cosmic rays become absorbed essentially within the upper few meters of the rock surface. Most cosmogenic nuclides occur in extremely low concentrations, requiring very sensitive detection techniques such as accelerator mass spectrometry.

For radioactive cosmogenic nuclides, concentration N [atoms g^{-1}] grows gradually with the duration of exposure, until after about five half-lifes ($t_{1/2}$) it reaches an equilibrium level Ng between production and decay. The "exposure age" of a sample, at first completely shielded from and later suddenly exposed to cosmic radiation, derives from the amount of the radioactive nuclides N according to

$$t = -\ln\left(1 - \ln 2/t_{1/2} * N/P\right) * t_{1/2}/\ln 2 \tag{8}$$

where P is the cosmogenic production rate of N. If a sample already at its level Ng is suddenly shielded from cosmic radiation, so that production is suspended, the nuclide content N declines by radioactive decay and the beginning of shielding, i.e., the "burial age," can be dated according to

$$t = \ln\left(N_g/N\right) * t_{1/2}/\ln 2 \tag{9}$$

The exact knowledge of the production rates of the various cosmogenic nuclides is a prerequisite for their dating application. These rates are derived by experimental measurements as well as theoretical calculations. The decrease from the poles to the equator is known as *latitude effect*. Also an *altitude effect* needs to be taken into account, since P increases strongly with altitude.

The analysis of ^{26}Al should always be combined with that of ^{10}Be (^{26}Al/^{10}Be method), in order to eliminate uncertainties about production rates. For the production rate ratio ^{26}Al/^{10}Be in quartz, a value of 6.1 was reported (Nishiizumi et al. 1989). Once the rock is shielded from further cosmogenic production, this ratio decays with an effective half-life of 1.36 ± 0.07 Ma, which enables its application in the 10 Ka to 10 Ma age range.

Burial dating with cosmogenic ^{26}Al and ^{10}Be was first applied to quartz gravels in caves for deriving river incision rates (Granger and Muzikar 2001). Later the hominin sites at Sterkfontein (Partridge et al. 2003) and Sima del Elefante at Atapuerca (Carbonell et al. 2008) were dated with this technique. ^{26}Al/^{10}Be burial dating of quartz-bearing sediments and artifacts from the lower strata of the Zhoukoudian karstic cave, where early representatives of *Homo erectus* were discovered, has been carried out by Shen et al. (2009). There, the sediment was transported by fluvial processes from the source into the cultural layers, ca. 20–25 m below the current surface at the time of occupation. The weighted mean age of three sediment samples and three quartzite artifacts gave 770 ± 80 Ka for the lower layers 7–10. However, these ages are substantially older than previous dating attempts (cf. uranium series and fission track).

Conclusion

Dating methods based on radioactive decay are in principle independent clocks, that is, they rely solely on the measurement of radiometric quantities, on known physical constants, and on natural isotopic abundances. The potassium–argon, fission-track, luminescence, electron spin resonance, uranium-series, and ^{26}Al/^{10}Be methods exploit such independent clocks. Radiocarbon, on the other hand, is a dependent clock, since it requires calibration by independently derived ages, for instance, by dendrochronology, varve chronology, and/or uranium-series dating.

Radiometric dating provides the baseline for calibration of other dating approaches, such as isotope stratigraphy, climate stratigraphy, bio-stratigraphy, and magneto-stratigraphy, as well as by astronomical and chemical means. All these latter techniques rely on natural changes with varying rates that are more or less predictable. Only through calibration do these techniques become chronometric tools.

During the last few decades, a solid chronology for the time since hominids entered the scene some five million years ago has been established through radiometric dating. Present methodological developments focus primarily on improving the time resolution of these methods, a prerequisite of deciphering natural and cultural processes. Paleoanthropological knowledge and concepts have greatly benefited from these advances.

Cross-References

- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Modeling the Past: Archaeology
- ▶ Origin of Modern Humans
- ▶ Overview of Paleolithic Archaeology
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- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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Patterns of Diversification and Extinction

Walter Etter

Contents

W. Etter (✉)
Abteilung Geowissenschaften, Naturhistorisches Museum Basel, Basel, Switzerland
e-mail: walter.etter@bs.ch; walter.etter@unibas.ch

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Abstract

The history of life on Earth, from the earliest microscopic cells to the modern world populated by the rich variety of animals, plants, fungi, and microbes, is more than 3,500 Myr long. Documenting the diversity patterns through the Proterozoic and Phanerozoic has been a major task in the past decades and is fraught with many methodological problems. The emerging picture is one of a very irregular increase in diversity. The most significant episodes of diversification occurred during the Cambrian–Ordovician and throughout the Mesozoic–Cenozoic. In the Phanerozoic alone, 5 major and more than 15 smaller mass extinctions disrupted the diversification of life and sometimes drastically altered the way of evolution. There was no common cause for these events, but all were the consequence of large-scale environmental perturbations. There is growing concern that we are currently entering a "Sixth" major extinction, caused by human impact on nature.

Introduction

This chapter reviews the history of diversity, the "ups and downs" of life, during the past 3,500 Myr. There are many reasons why the history of life's diversity on Earth is an important avenue of paleontological research. (1) Such studies can give us insight into the relative importance of various mechanisms of evolution. (2) The analysis of diversification and extinction can help to clarify the respective roles of biotic (intrinsic) versus abiotic (extrinsic) factors. (3) The importance of regional versus global patterns/mechanisms can be investigated. (4) The analysis of extinctions might enable us to see if there are common patterns. (5) The possibility that *Homo sapiens* is causing yet another mass extinction fosters interest in other such events in the geological past.

One emergent theme when documenting patterns of diversification and extinction is that the major disruptions/discontinuities were not the consequence of some lineages' "racial senility" or "genetic exhaustion" but rather caused by large-scale environmental perturbations. The world as we know it today, with its current climatic and atmospheric conditions and present-day biosphere, is not a good actualistic example for the remote past, where sea levels and mean annual temperatures were vastly fluctuating, continental plates had entirely different positions, and CO_2 and O_2 levels in the atmosphere showed secular changes.

This chapter is organized as follows:

- First, an overview of major events in the history of life is given, together with an overview of changes in abiotic conditions. Here some emphasis is placed on the Precambrian.
- The patterns of diversification of Phanerozoic life are reviewed, most extensively for marine animals with preservable hard parts.

- Methodological problems in documenting diversity (as a measure of taxonomic richness) through time are discussed.
- In a special subchapter, some of the most important radiations and extinctions are treated in stratigraphic order.

A Short History of Life on Earth

According to the newest dating, the Earth is 4,567 Myr old (Fig. 1; Van Kranendonk 2012). Already ~4,500 Myr ago, the planet experienced probably its most dramatic event: the impact of the mars-sized protoplanet "Theia" led to the formation of the moon (Taylor 2007). Between 4,500 and 4,400 Myr ago, the Earth changed from a planet with a liquid magmatic surface to one with a solid surface. Some detrital zircon grains from the Jack Hills in Australia are up to 4,400 Myr old, and their composition might indicate that liquid water and a thin crust were already present at that early date (Wilde et al. 2001; Van Kranendonk 2012). The oldest rocks currently recognized (Acasta gneiss from the Northwest Territories, Canada) are dated as 4,030 Myr (Nelson 2004). The earliest Eon of Earth history, the Hadean, thus left no directly observable documents. It is nowadays assumed that the initially high temperatures following the accretion of the Earth had dropped by around 4,400–4,000 Myr ago to below 100 °C. During the earliest Archean, the surface temperature was probably quite low (faint early sun). By that time, liquid water was present on the Earth's surface, brought to the planet by icy asteroids (Kramers 2007). Yet, the "heavy bombardment" with bodies exceeding 250 km in diameter lasted until 3,800 Myr ago (Late Heavy Bombardment (LHB) between 3,900 and 3,800 Myr ago; Van Kranendonk 2012). This must have led to repeated boiling of the oceans and the vaporization of their water (Nisbet and Sleep 2001, 2003).

Contrary to earlier beliefs (e.g., those assumed in the famous Miller experiment), most researchers today think that the Hadean and Early Archean atmosphere was only mildly reducing, with mainly CO_2 and N_2 present but also smaller amounts of CH_4, NH_3, and H_2 (McClendon 1999; Raven and Skene 2003; McCollom 2013). Free oxygen perhaps built through photodissociation of water vapor in the upper atmosphere, but quickly reacted with Fe^{2+} and other unoxidized compounds. The early atmosphere was therefore devoid of free oxygen (McClendon 1999; Miller and Lazcano 2002; Westall 2012).

Under these conditions life originated (for reviews, see Oró et al. 1990; Brack 1998; McClendon 1999; Fenchel 2002; Taylor 2005; Deamer 2011; Westall 2012). Organic compounds could form in the atmosphere through UV-photolysis, electrical discharges, and major impact shocks (McClendon 1999; Lazcano 2001; McCollom 2013), and a major source of organic molecules was probably also comets and interplanetary dust (Lazcano 2001; Miller and Lazcano 2002). But early life certainly evolved in the sea (Raven and Skene 2003; Westall 2012). It is now widely assumed that an RNA world preceded life based on proteins and DNA (Lilley and Sutherland 2011; Gargaud et al. 2012). The first cells were probably

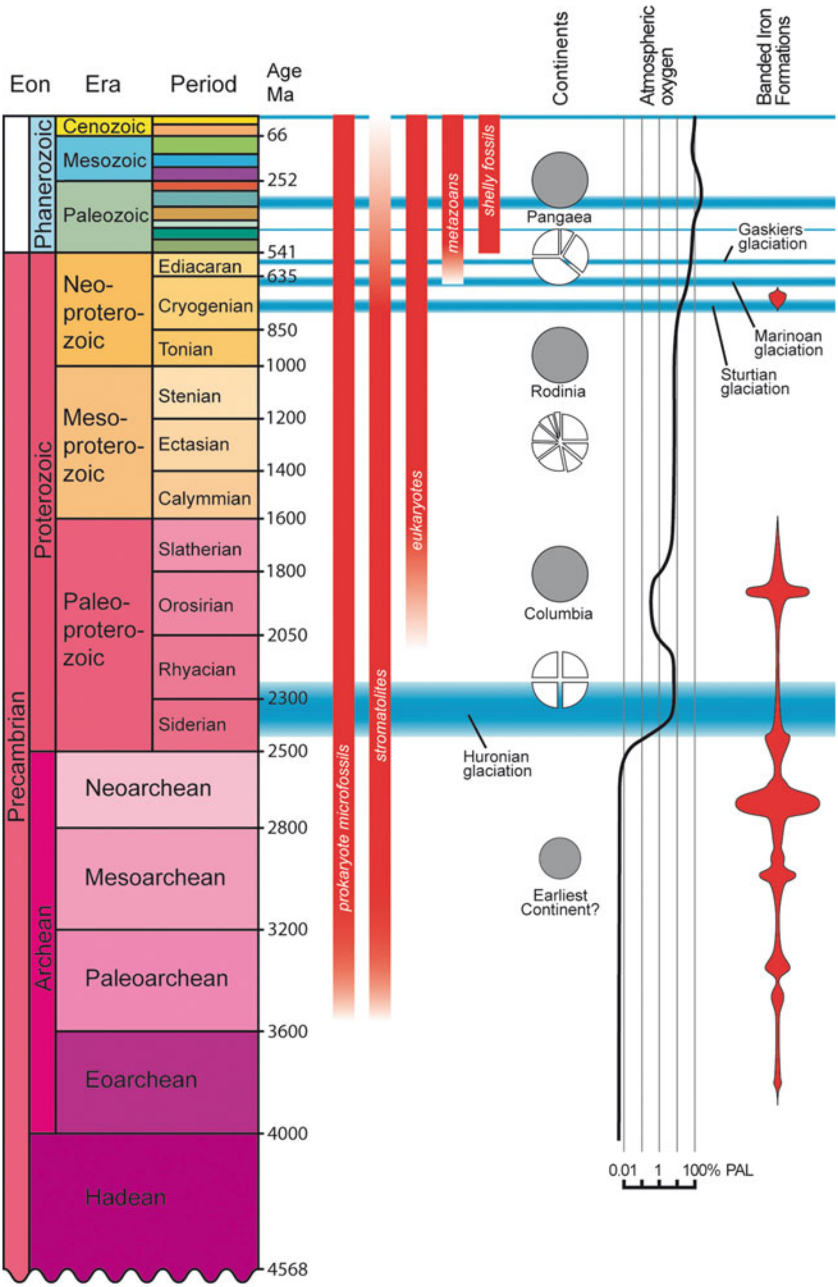

Fig. 1 Major events in earth history in the Precambrian (Modified after various sources)

heterotrophs (Lazcano and Miller 1996; Peretó 2011; but see Huber and Wächtershäuser 1997; Wächtershäuser 2000, 2006). As possible sites where cellular life evolved from prebiotic precursors, continental thermal springs, volcanic vents, warm hypersaline lagoons (Darwin's "warm little pond"), and deep submarine vents are the most likely candidates (Schopf 1999; Westall 2012). In this respect it is noteworthy that the earliest branches of both the Archaea and Bacteria are thermophilic (Pace 1997). Yet, an extraterrestrial origin of cellular life cannot totally be excluded ("Panspermia"; Horneck 2003).

Perhaps life originated sequentially several times, but was always exterminated by the heavy meteorite bombardment ("impact frustration"; Schopf 2002). Yet, all life on Earth shares a common origin (Theobald 2010). The "Last Universal Common Ancestor" (LUCA) might have been a diverse community of cells that experienced extensive horizontal gene transfer (Woese 1998, 2002; Glansdorff et al. 2008). Organismal lineages established themselves with the subsequent splitting into the three domains "Bacteria", "Archaea," and "Eukarya" (Woese 1998). The tree of life is thus at its base a web (Doolittle 1999) or even a ring (Rivera and Lake 2004).

The fossil record of the Archean is notoriously sparse. The presumed oldest cellular microfossils come from 3,500- to 3,450-Myr-old sediments in Western Australia (Schopf 1992a, 1993, 2004, 2006; Van Kranendonk et al. 2008; De Gregorio et al. 2009; Schopf and Kudryavtsev 2012; but see Brasier et al. 2004; Wacey 2009; Wacey et al. 2009). Almost as old (3,400–3,200 Myr) are microfossils in the metasediments of the Onverwacht and Fig tree groups (South Africa). Putative microfossils (*Isuasphaera*) were described (Pflug 1978) from even older (3,800 Myr) metamorphosed sedimentary rocks from Greenland (Isua Greenstone Belt) but are probably of inorganic origin (Bridgwater et al. 1981; Appel et al. 2003).

According to most authors (Mooers and Redfield 1996; Sheridan et al. 2003; Hedges 2009), the split between bacteria and archaea–eukaryota must have occurred more than 3,500 Myr ago. The Proterozoic fossil record (Hofmann and Schopf 1983; Mendelson and Schopf 1992; Schopf 1992a, b) documents an increasing diversification and complexity of cells, but the evolution of metabolic pathways cannot be deduced from the morphology of the microfossils. Yet, by 2,700 Myr ago, oxygenic photosynthesis, methanogenesis, and methylotrophy had probably developed, perhaps also sulfate reduction and nitrogen fixation (Buick 2001; Sleep and Bird 2007; Copley and Summons 2012).

In contrast to cellular fossils, the record of stromatolites is quite good. These are biosedimentary structures built by microbial mats which trap sediment particles (Riding 1991, 2000; Walter 2001; Bosak et al. 2013). The oldest stromatolites date from 3,500- to 3,200-Myr-old sediments in Australia and South Africa (Wacey 2009; Van Kranendonk 2012), but their fossil record remains spotty until the Neoarchean (Walter 1983, 2001; Grotzinger and Knoll 1999). They diversified considerably in the Proterozoic, and in the Mesoproterozoic a large number of different types had developed, growing sometimes to impressive sizes

(Awramik and Sprinkle 1999; Walter 2001; Riding 2006a). Stromatolites declined both in diversity and abundance in the terminal Proterozoic, and in the Phanerozoic they remained largely restricted to marginal marine environments (Riding 2006a, b). This decline was traditionally seen as a consequence of the rise of the metazoans, which consumed the microbial mats (Mata and Bottjer 2012), but it might also have abiotic reasons (Awramik and Sprinkle 1999; Riding 2006a, b).

Significant changes in the carbon and sulfur isotope signatures of rock and kerogen samples in the latest Archean between 2,750 and 2,500 Myr ago point to increased microbial productivity and rapid crust formation. For some time, biological and geological processes were out of equilibrium (Van Kranendonk 2012). Between 2,400 and 2,200 Myr ago, the atmosphere changed rather abruptly from reducing ($pO_2 < 0.01$ % present atmospheric level PAL) to oxidizing ($pO_2 > 1$ % PAL; Fig. 1), largely as a result of the activities of oxygenic photoautotrophs (Schopf 1992a; Holland 1994; Canfield 2005; Van Kranendonk 2012; for alternative scenarios of atmosphere evolution, see Ohmoto et al. 2004). This is known as the "Great Oxidation" in the Early Proterozoic (Goldblatt et al. 2006). Until about 2,400 Myr ago, free oxygen was constantly removed by oxidation of weathered reduced minerals (Nisbet and Sleep 2001; Lenton 2003; Goldblatt et al. 2006). Detrital pyrite and uraninite are common until 2,200 Myr ago and indicate still very low levels of free oxygen; otherwise these minerals would have been oxidized (Schopf 1992a; Holland 1994). Likewise, the genesis of banded iron formations (BIFs), which are absent in rocks younger than 1,700 Myr, requires reducing conditions in the deeper parts of the seas (Simonson 2003; Van Kranendonk 2012).

From 2,450 to 2,200 Myr ago, the Earth witnessed the first well-documented ice age, the "Huronian" or Makganyene glaciation (Pierrehumbert et al. 2011). As a consequence of insufficient time resolution, the exact duration of glacial intervals during this Paleoproterozoic time period is unknown (Young 2004; Van Kranendonk 2012). The onset and the termination seem to have been gradual (Young 2004). Perhaps the increase in atmospheric oxygen was the cause of the Huronian glaciation (Kopp et al. 2005). If methane was a major contributor to a greenhouse effect prior to that time, it would have been oxidized in a more oxygen-rich atmosphere, and the removal of this greenhouse gas could well have led to global cooling and the onset of an ice age. However, the causes of the Early Proterozoic glaciation are still debated (Van Kranendonk 2012).

The origin of the eukaryotes can be placed at some time before 2,100 Myr ago. Large and unquestionably eukaryotic acritarchs are known from 1,800-Myr-old rocks (Lamb et al. 2009), and the macroscopic "algae" *Grypania* is most likely also a eukaryote, putting the oldest eukaryotic record to 2,100 Myr (Han and Runnegar 1992). Eukaryote-specific biomarkers were even reported from 2,700-Myr-old metasediments of Western Australia (Brocks et al. 1999) but proved to be contaminants (Fischer 2008). Perhaps the origin of eukaryotes was linked to the increased oxygen content of the atmosphere and shallow waters where a nucleus and its protective membrane would be advantageous (Dyer and Obar 1994). Subsequent evolution of the eukaryotes took place by serial endosymbiosis (Margulis 1981) in which engulfed α-purple bacteria became mitochondria and cyanobacteria became plastids (Dyer and Obar 1994; Pace 1997). In part, even secondary and tertiary endosymbiosis must have occurred in which photosynthetic eukaryotes were engulfed by nonphotosynthetic eukaryotes (Woese et al. 1990; Chan and Bhattacharya 2010).

Little is known about the early evolution of the eukaryotes (Knoll et al. 2006). Apart from the acritarchs that are a heterogeneous assemblage of planktonic, unicellular eukaryotes known from the Late Paleoproterozoic and extending into the Phanerozoic (Martin 1993; Knoll 1994), other fossils of the eukaryotic clade include various carbonaceous films that are not easy to interpret (Hofmann 1994; Knoll et al. 2006). Judged from isotopic signatures and sedimentologic features, between 1,800 and 800 Myr ago was a time of environmental stability that has been dubbed "the boring billion" or "Earth's dullest period of time" (Buick et al. 1995). Yet, this was also the time of formation of the supercontinent Rodinia and of major diversification of eukaryotes (Van Kranendonk 2012). New molecular dates, which are in reasonable agreement with paleontological findings, give some clues as to when new groups originated. The divergence between protists and crown-group plants may be as young as 1,300–1,100 Myr, the origin of the fungi is placed at 1,200–1,000 Myr ago, the split between choanoflagellates and eumetazoans occurred 1,000–900 Myr ago, and the first bilaterians made their appearance 900–700 Myr ago (Douzery et al. 2004; see also Peterson et al. 2004, 2008; Peterson and Butterfield 2005; Bhattacharya et al. 2009; Blair 2009; Erwin et al. 2011).

Between 800 and 600 Myr ago in the Cryogenian period, the Earth witnessed several large glaciations. The last two episodes are well dated. The Sturtian glaciation occurred around 715 Myr ago and the Marinoan ("Varanger") glaciation around 635 Myr ago (Allen and Hoffman 2005; Pierrehumbert et al. 2011; Shields-Zhou and Och 2011). Some, perhaps most, continental land masses had near-equatorial positions at that time. Glaciers might have reached equatorial regions and perhaps extended down to the sea level. According to the most dramatic scenario (Hoffman et al. 1998; Hoffman and Schrag 2002; Hoffman 2009; but see Chandler and Sohl 2000; Poulsen 2003), temperatures initially dropped due to some unknown mechanism, but as soon as glaciers reached a critical extension in low latitudes, enough solar energy was reflected back into space that ice sheets could grow at an ever-increasing rate. In this "runaway albedo" model, not only all the land masses became ice covered, but the surface of the oceans were also globally frozen ("snowball earth"; Kirschvink 1992; Hoffman et al. 1998; Hoffman and Schrag 2002). The seas became anoxic and BIFs could accumulate again (Hoffman et al. 1998). Eventually, enough volcanic CO_2 accumulated, and the glaciations ended abruptly. Later Neoproterozoic glaciations are documented, but these did not reach equatorial regions (Pierrehumbert et al. 2011; Shields-Zhou and Och 2011).

Shortly after the last of these major Neoproterozoic glaciations, the first metazoans enter the fossil record. Enigmatic soft-bodied fossils 580–541 Myr old are known from localities around the world and named Ediacara assemblages (after the Ediacara Hills in South Australia). Although the nature of the flattened, segmented, or quilted Ediacara organisms is still disputed (mainly cnidarians and annelids

(Glaessner 1983, 1984; Jenkins 1992) or organisms not related to any of the extant animal phyla (Seilacher 1989, 1992; Buss and Seilacher 1994)), they are accompanied by traces produced by bilaterian metazoans (Knoll and Carroll 1999; Valentine et al. 1999; Martin et al. 2000; Erwin and Valentine 2013). Yet, tracemakers were small and rare and did not disrupt the sediment. This only changed near the Precambrian–Cambrian boundary when bioturbation markedly increased, and the sediment became unstable (Erwin and Valentine 2013). This probably led to the extinction of the immobile Ediacara organisms (Seilacher 1999).

Within a short time after the beginning of the Cambrian at 541 Myr, the most remarkable episode in the history of life started, the so-called Cambrian explosion. Within only 20 Myr, all animal phyla with preservable hard parts (with the exception of the bryozoans) appeared (Knoll and Carroll 1999; Erwin 2001a; Valentine 2002, 2004; Erwin and Valentine 2013). With the beginning of the Cambrian, and continuing throughout the Phanerozoic (Fig. 2), we have a very reliable fossil record especially for the marine invertebrates with easily preservable hard parts. Fossiliferous localities that show exceptional preservation are interspersed in the stratigraphic record and provide us with information on the soft-bodied fauna (Bottjer et al. 2002; Seldon and Nudds 2012). Information on the Phanerozoic history of life can be found in many textbooks on paleontology, evolution, and historical geology (Stanley 2009; Cowen 2013; Monroe and Wicander 2011; Storch et al. 2013), and extensive treatment is beyond the scope of that chapter. Details on selected episodes of radiation and extinction are given in the last part of this chapter.

During the Cambrian, life was exclusively marine and dominated by trilobites and a variety of other arthropods. Because the trilobites were highly diverse, are easily determined, and show a high species turnover, trilobites are the most important index fossils for this period. Brachiopods were small and belonged mostly to the inarticulate groups. Among the mollusks, hyoliths and monoplacophorans were the most conspicuous, but in the Late Cambrian, the first small nautiloids appeared, marking the beginning of a highly successful group of marine predators. Cambrian echinoderms belonged mostly to groups that were immobile and became extinct during the Early Paleozoic. Already during the Early Cambrian, the first true reefs built by the spongelike archaeocyathans developed, but archaeocyathans became extinct at the end of the Early Cambrian, leaving a reef gap until the Middle Ordovician. The first chordates and agnathan fishes appear to have been rare, with the exception of the conodonts.

The extinction events in the Late Cambrian affected most severely the trilobites and several echinoderm groups. Ordovician and Silurian seas became dominated by articulated brachiopods and stalked echinoderms (crinoids and blastoids). Although the first deep burrows appeared at that time, life was still mainly epibenthic. Large reefs dominated by tabulate and rugose corals and stromatoporoids developed, and bryozoans became an important component of marine hard bottoms. Among the planktonic organisms, the graptolites diversified considerably and have proven to be the most valuable index fossils for the Ordovician and Silurian. Large predators developed among the nektonic nautiloids and among the eurypterids.

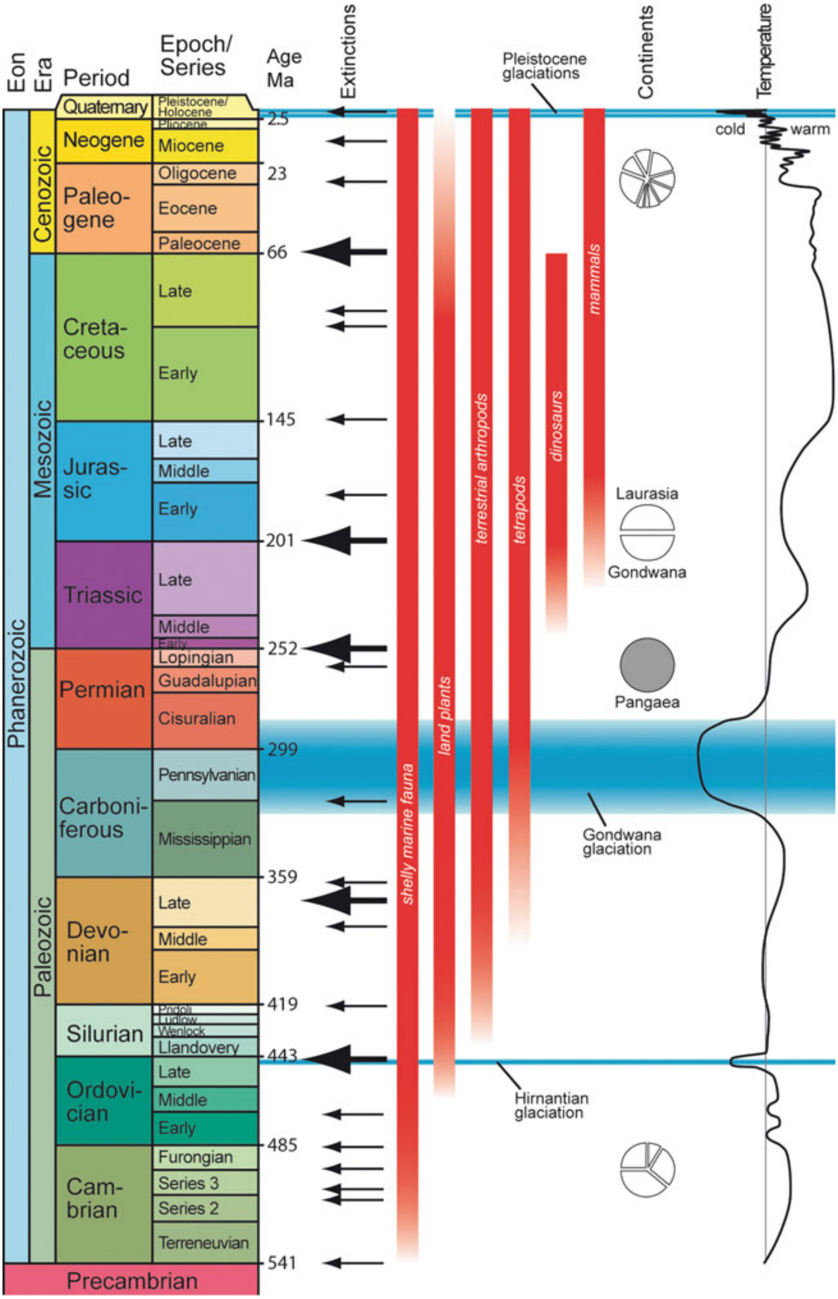

Fig. 2 Major events in earth history in the Phanerozoic (Modified after various sources)

Several groups invaded freshwater environments, among them the arthropods and various fish groups. Colonialization of the land started in the Ordovician–Silurian, first by plants (although algal crusts and fungi may have been present earlier), then by mites, arachnids, millipedes, and scorpions. Among the vertebrates, the appearance of the first jawed fishes in the Late Silurian was a major innovation.

During the Devonian and Carboniferous, land plants diversified in an explosive manner leading to the first true forests, and the first seed plants had developed by the Carboniferous. The first wingless insects appeared in the Early Devonian, but it was not until the Carboniferous that the first winged insects conquered the air. In the vertebrates, huge marine predators developed among the placoderms. The Devonian, also called the "age of fishes," saw the first appearance of the chondrichthyans and actinopterygians, while the agnathans considerably diversified. The first tetrapods appeared during the Middle–Late Devonian, and the amniote egg evolved in the Late Carboniferous. Among the marine benthic organisms, tabulate–rugose–stromatoporoid reefs attained a new climax. Articulate brachiopods and stalked crinoids still dominated most seafloors. Among the nektonic organisms, the evolution of the ammonoids was a major innovation during the Early Devonian. This group provided the most important index fossils for the Devonian to Cretaceous periods. In the latest Paleozoic, life in the seas did not radically change, but the absence of the heavily armored fishes is notable, and among the cephalopods the stoutly shelled nautiloids also declined, while the ammonoids flourished. Reef building was confined to smaller constructs after the Late Devonian mass extinction. On land, the mammal-like reptiles were the dominant herbivores and carnivores.

After the end-Permian mass extinction, life in the seas and on land dramatically changed. Seafloors were no longer dominated by epifaunal brachiopods and crinoids but by gastropods and burrowing bivalves. Reef production came to a halt during the Early Triassic, and it was not until the Middle Triassic that scleractinian coral reefs became established. This type of reef building would dominate throughout the rest of the Mesozoic and Cenozoic. Only during part of the Cretaceous were the corals replaced as principal reef builders by a group of aberrant bivalves, the rudists. The open waters were dominated by ammonoids and actinopterygian fishes, and during the Mesozoic three groups of planktonic organisms which play an eminent role in biogeochemical cycles made their appearance: the planktonic foraminifers, the coccoliths, and the diatoms. The largest creatures of the seas, and the top predators, were the marine reptiles: nothosaurs, plesiosaurs, ichthyosaurs, marine crocodiles, turtles, and mosasaurs.

On land, the conifers, cycads, and ginkgos flourished and dominated the forests until the late Early Cretaceous when they became increasingly replaced by the flowering plants (angiosperms). Among the amphibians, the last stegocephalians died out, while the first frogs and salamanders appeared. After the end-Permian mass extinction, the mammal-like reptiles had become marginal players, and the archosaurs, most notably the dinosaurs, became the rulers of the Earth. The pterosaurs were the first vertebrates to conquer the air, by the Late Triassic; and in the Late Jurassic, the first birds evolved. Mammals arose already during the Late Triassic, but remained mostly small and peripheral throughout the Mesozoic.

The mass extinction at the Cretaceous–Tertiary boundary, although much less severe than the extinction at the end of the Permian, nevertheless severely altered the structure of both marine and terrestrial ecosystems. In the seas, the shelled cephalopods became entirely extinct with the exception of a small group of nautilids, and among the marine reptiles, only the turtles survived. The vacant ecospaces were filled up by actinopterygian fishes and mammals. The mammals also played a central role in the restructuring of the terrestrial communities. During the remarkable radiation in the Paleogene, mammals occupied almost all available niches on land, invaded the seas (whales, pinnipeds, sea cows), and conquered the air (bats). Birds equally radiated considerably, and in some regions, large, flightless birds even became the top predators. After the Eocene–Oligocene climatic revolution, the flora and fauna had an essentially modern organization, and grasses as the most important terrestrial producers became widespread during the Miocene. The Miocene radiation of the apes ultimately led to the development of our species, *Homo sapiens*.

Directionality Versus Contingency

During the Precambrian, eukaryotes evolved from prokaryotes, and in the Cambrian, most animal phyla evolved. Ever more environments were colonialized during the Phanerozoic, including the land and the air. For the evolution of the vertebrates, the long-portrayed succession of the "age of fishes," "age of reptiles," and "age of mammals" is of course a gross oversimplification. Osteichthyans and chondrichthyans were never as diverse as today! Yet, although measuring morphological complexity is not straightforward, there was clearly a trend toward increasing complexity in the evolution of life from bacteria to today's biota (Carroll 2001; Rosslenbroich 2006; McShea and Brandon 2010; Korb and Dorin 2011).

There are two fundamentally different views on this complexity increase. According to one view, the rise and ultimately dominance of complex life forms were an inevitable outcome of natural selection, whereby more complex organisms outcompete the more primitive ones. It also inevitably culminates with the development of intelligent animals. Such a view is championed, e.g., by Conway-Morris (1998, 2003) and is reminiscent of an Aristotelian "chain of being."

A radically different view of the evolution of life does not see complex mammals as superior to bacteria. The increase in diversity is not neglected, but is explained in a different way. Bacterial cells cannot evolve toward ever-smaller sizes, unicellular eukaryotes cannot evolve toward zero cells but only toward multicellularity, and marine organisms cannot evolve to colonialize a nonexisting environment, although they can evolve land-dwelling species and among animals also flying taxa. The evolution toward greater complexity is thus simply a move away from an "impermeable left wall" and an increase in variance; but in a sense we still live in a bacteria-dominated world (Gould 1996).

Perhaps the truth lies somewhere in between. There is no necessity to evolve toward intelligence, but ultimately this was made possible through successive evolutionary steps after the increasing variance crossed several thresholds.

In such a view, life on Earth followed a megatrajectory along the following sequence (Knoll and Bambach 2000): prokaryote diversification (including metabolic pathways, but inability for sexual reproduction), early eukaryote diversification (first consumers, multicellularity, increased size, sex), aquatic multicellularity (large size, packaging of biomass, fast movement, complex food chains), invasion of the land (huge biomass of producers, adaptation to widely fluctuating environments), and ultimately intelligence (which perhaps could also have evolved in the water). Nevertheless, if “life’s tape were replayed,” the outcome would certainly be totally different (Gould 2001).

Diversity Patterns: The Broad Picture

The Textbook Version

The last decades have witnessed a veritable boom of publications documenting the diversity patterns of life during Earth history and the pace of large-scale evolution. Outstanding contributions came especially from the late “Jack” Sepkoski. His 1981 curve of Phanerozoic diversity patterns of marine families (and subsequent refinements down to the genus level; Fig. 3; Sepkoski 1996, 1997, 2002) is one of the most often reproduced figures in the paleontological literature (equaling perhaps the Berlin *Archaeopteryx* specimen; Benton 2001), and this benchmark is an ideal starting point for the discussion of life’s ups and downs during the last 541 Myr.

Assembling literature-based compilations of the worldwide temporal distribution of marine families (Sepkoski 1982, 1992) and genera (Sepkoski 2002), the number of described taxa and hence diversity for every successive stratigraphic interval (usually stages) could be determined. In addition, the times of origination (first occurrence) and extinction (last occurrence) of these taxa could be deduced.

By means of a factorial analysis, Sepkoski (1981) could show that the marine families grouped into three rather well-delineated entities each showing a common pattern of origination, diversification, and decline. These three “evolutionary faunas” were called “Cambrian fauna,” “Paleozoic fauna,” and “Modern fauna” (Sepkoski 1981). A division into finer intervals (nine “Ecological Evolutionary Units”) was suggested by Boucot (1983) and further refined by Sheehan (1996, 2001a); yet, these intervals mainly portray ecological communities and not evolutionary units.

According to Sepkoski’s figures, diversity at the family level shows a sharp rise at the beginning of the Cambrian, continuing well into the Middle Cambrian. In the Middle Cambrian, a plateau was reached, and several drops in diversity occurred. The main representatives of this Cambrian fauna were trilobites, inarticulate brachiopods, hyolithids, monoplacophorans, archaeocyathids, and eocrinoids (Sepkoski 1981, 1984). During the Early Ordovician, diversity increased again to reach a level about three times that of the Cambrian. Responsible for that fast and unprecedented increase in diversity were members of the Paleozoic fauna, mainly

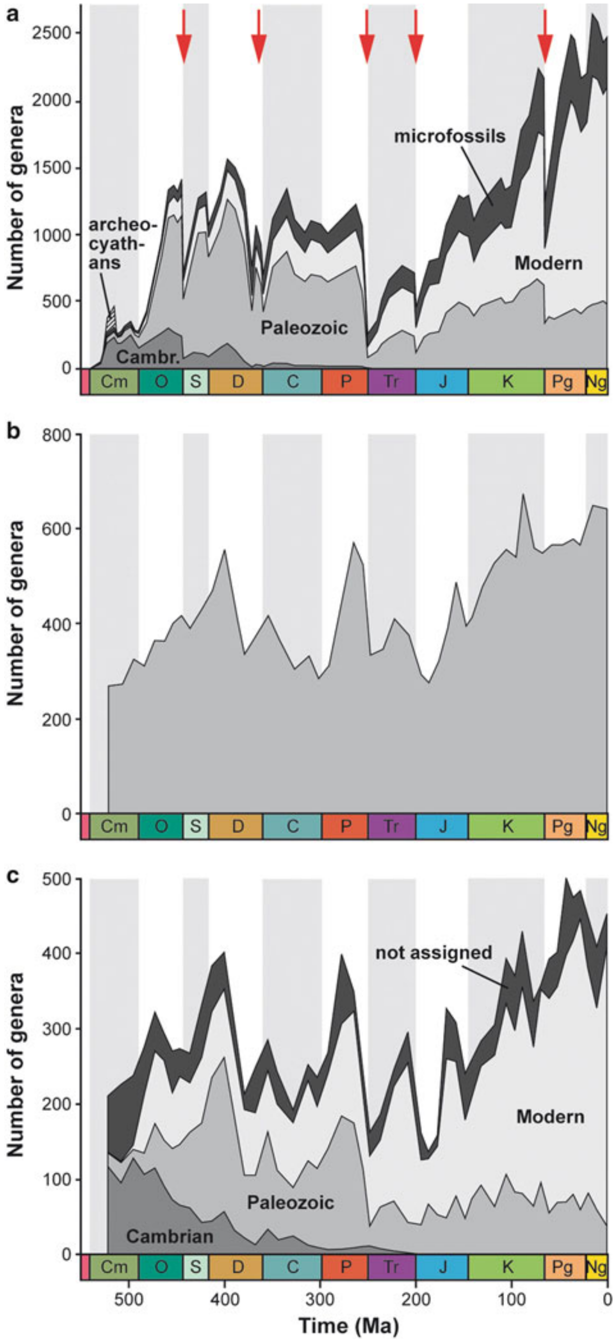

Fig. 3 Genus diversity over the Phanerozoic ((**a**) After Sepkoski 1997; (**b**) After Alroy et al. 2008; (**c**) After Alroy 2010)

articulate brachiopods, crinoids, rugose and tabulate corals, ostracods, cephalopods, bryozoans, asteroids, ophiuroids, and graptolites. The diversity reached by the Ordovician radiation remained almost constant through the rest of the Paleozoic, interrupted only by punctuations of extinctions and subsequent recoveries.

The Late Permian witnessed a dramatic extinction pulse, and the members of the Paleozoic fauna lost their dominance. The Modern fauna (demosponges, bivalves, gastropods, gymnolaemate bryozoans, and malacostracan crustaceans) had its origins in the Paleozoic, but its members remained a minor component up to the Permian. During the Triassic, Jurassic, and Cretaceous, members of the Modern fauna originated at a considerably faster rate than members of the Paleozoic fauna, and overall diversity increased steadily throughout the Mesozoic. The end-Cretaceous extinction appears at the family level only as a minor perturbation, and the diversity increase continues throughout the Cenozoic. By the end of the Neogene, family diversity had reached a level almost twice that of the Paleozoic.

The taxic diversity trends observed by Sepkoski were accompanied by several other notable trends which relate to the structuring of marine communities. During the Phanerozoic, the species numbers within open marine assemblages increased through time (denser “species packing”; Bambach 1977), and between the three evolutionary faunas, a significant increase in the number of feeding types and occupied substrate niches (“guilds”) is documented (Bambach 1983). In addition, the proportion of mobile taxa and of predators increased (Bambach et al. 2002; Bush and Bambach 2011). This is paralleled by changes in the spatial structure of marine benthic communities. Animals of Cambrian communities neither extended high above nor burrowed deep into the substrate, but during the mid-Paleozoic to mid-Mesozoic, many suspension feeders evolved that stood highly erect above the substrate, and several tiers of epifaunal benthos developed (Ausich and Bottjer 1982; Bottjer and Ausich 1986; Signor 1990; Bush and Bambach 2011). A complex tiering, as documented by trace fossils, also developed among the burrowing endobenthos, although very deep burrows only became common in the latest Paleozoic.

Following the broad interest in the Phanerozoic diversity trajectories documented for marine animals, various researchers also published figures for other groups of organisms (for earlier work, see Valentine 1985). For insects, a synoptic curve for the number of families was published that shows an increase in diversity from the Devonian to the recent. The only notable event that led to a significant decrease in the number of families seems to be the end-Permian mass extinction (Labandeira and Sepkoski 1993; Labandeira 1999). Extensive data have also been assembled for fishes (Lloyd and Friedman 2013) and tetrapods (Benton 1993; Benton et al. 2013). Here, the most significant outcomes are an only slight overall diversity increase from the Devonian to the Late Cretaceous and a huge increase in the number of families after the end-Cretaceous extinction (Benton 1999; Fig. 4). Plants differ from the various animal groups in that the family richness over the Phanerozoic follows a much smoother path, and extinctions had little effect on family diversity (Niklas 1997). At lower taxonomic levels, however, plants also suffered heavily from mass extinctions (McElwain and Punyasena 2007).

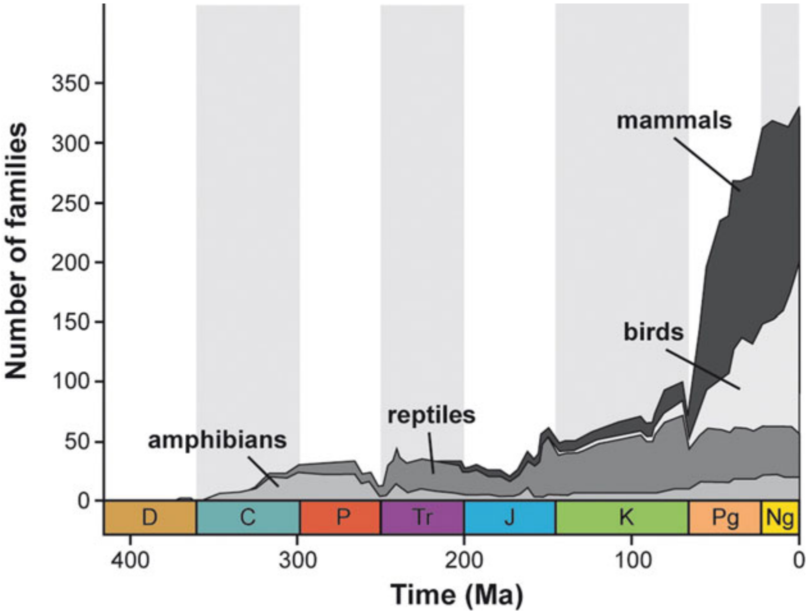

Fig. 4 Phanerozoic family diversity in tetrapods (After Benton 1999)

Methodological Problems and Newer Developments

The documentation of Phanerozoic diversity patterns goes back to Phillips (1860), who used data from marine rocks in Great Britain to distinguish between Paleozoic, Mesozoic, and Cenozoic life, and showed that diversity increased throughout the Phanerozoic (see Miller 2000). Renewed interest in these large-scale patterns arose in the 1960s and 1970s, stimulated especially by the pioneering publications of Gregory (1955), Simpson (1960), and Newell (1967). The first diversity patterns published thereafter (Valentine 1969; Raup 1972, 1976a, b; Bambach 1977) showed mainly that this was a very difficult task. The results were, in part, grossly dissimilar, especially with respect to the diversity increase in the Cenozoic. Although a "consensus paper" was published shortly thereafter (Sepkoski et al. 1981), discussions of methodological problems continue. The interpretations of Phanerozoic diversity patterns have thus fluctuated between two extremes: it might be the real picture or an artifact of databases affected by different and heavy biases.

A first problem is how to count. Should we omit taxa that occur in only one time bin? This would prevent taxa known only from Fossil-Lagerstaetten or a single monograph from summing up to exceptional high diversity in that time bin (Foote 2000). On the other hand, omission of single occurrences can exclude whole groups of short-lived taxa. There may be problems with the taxonomic databases used, which can add noise and possibly induce false signals (Signor 1985). Yet, two databases at the family level compiled by Sepkoski (1982, 1992) and a team of specialists (Benton 1993) produced very similar results. A further problem is unsampled ranges. A taxon can extend further back in time ("ghost range") and also reach further upward ("zombie lineages") than recorded in the database (Lane et al. 2005). Ghost ranges can potentially be elucidated with a phylogenetic approach, whereas zombie lineages cannot. Correcting for these errors has hitherto met with limited success (Lane et al. 2005). The "pull of the recent" is another potential source of error and refers to the fact that the modern biota is much more completely sampled than fossil strata. Therefore, it tends to extend the stratigraphic ranges of extant families, or species that are known from some time in the Cenozoic, through intervals where fossils of those taxa are missing. This bias was either seen to be a negligible quantity (Jablonski et al. 2003) or a major source of bias (Alroy et al. 2008; Aberhan and Kiessling 2012).

Uneven sampling in different regions and in different periods is a fact that cannot easily be corrected for (Smith 2003). All the compendia are heavily biased toward occurrences in Europe and North America, with the important side effect that from the Jurassic onward tropical environments are underrepresented (Aberhan and Kiessling 2012). Uneven time spans of the sampled intervals (usually stages) are a further problem. To correct for this, longer stages are subdivided, and very short ones are amalgamated (Sepkoski 1996). Taphonomic biases (differential preservation) are usually thought of as occurring randomly through the Phanerozoic (Kidwell 2005; Cooper et al. 2006) although this is contentious (Alroy et al. 2008). But potential biases can occur, e.g., through taxa that are only rarely preserved (in extraordinary deposits, see above), producing a local peak in diversity for that stratigraphic interval (Sepkoski 1996). Culling of the data by removal of single occurrences (taxa that are confined to a single time bin) is the common procedure to remove this bias (Sepkoski 1996). Cenozoic samples are, on average, less often lithified than Paleozoic or Mesozoic ones (Hendy 2009) and therefore yield more fossils than their lithified counterparts. This again, like the "pull of the recent," will lead to an overestimation of the Cenozoic diversity increase (Alroy et al. 2008).

Perhaps the most distracting factor when analyzing diversity patterns is that the sedimentary rocks available for study are not evenly dispersed through the Phanerozoic (Raup 1972, 1976b; Ronov 1983; Peters and Foote 2001; Smith 2001; Smith and McGowan 2011). There is a correlation between sedimentary rock volume and apparent diversity, although its extent is still debated. Are the diversity trajectories real and independent of the outcrop area/sediment volume (Miller 2000), or does the close match even suggest a common cause for diversity increase and patterns of sedimentation (Hannisdal and Peters 2011)? Or does the correlation point to an important bias (Smith 2007) that needs to be corrected for?

There are many more problems surrounding the analysis of Phanerozoic diversity trajectories (Sepkoski 1996; Smith 2007; Alroy et al. 2008; Aberhan and Kiessling 2012). Several of these cannot be addressed using the existing compendia, and it was felt necessary to develop a new database. The Paleobiology Database (PBDB) is a huge collection of locality-specific inventories in the Phanerozoic record (Alroy et al. 2001, 2008; Adrain and Westrop 2003; Miller 2003; Aberhan and Kiessling 2012). Hopefully, the PBDB will allow for a much better correction of taphonomic and sampling bias (Alroy et al. 2001; Bush et al. 2004); will yield new insights into the respective contributions of alpha, beta, and gamma diversity to the Phanerozoic taxonomic richness (Bush and Bambach 2004); and will enable us to dissect geographical components of diversity changes.

Two global diversity curves for the Phanerozoic using subsampling methods of the PBDB have been published (Alroy et al. 2008; Alroy 2010). These show important differences from the Sepkoski curve (Fig. 3): Paleozoic diversity was probably underestimated in earlier curves, and the diversity increase during the Cenozoic was much less pronounced. However, the PBDB suffers also from inherent limitations, and some maintain that currently it is not a good reflection of the fossil record (Krug et al. 2009; Erwin 2009; Marshall 2010). The differences between the 2008 and 2010 curves also show that there is still some way to go until a new consensus is reached (Marshall 2010).

Expansion and Equilibrium Models

The interpretations of Phanerozoic diversity trajectories have remained problematic. For the increase in familial and generic diversity, three basic models derived from population ecology can be invoked to explain the pattern (Miller 1998; Benton 2001). First, if rates of species origination and extinction are unconstrained by existing diversity, and origination exceeds extinction rates, an exponential increase in taxic diversity will result, only interrupted by major extinction intervals. The second, linear model of diversity increase requires the addition of a fixed number of taxa in each unit time. This would require a constant decrease in the rate of evolution (speciation) or a regularly increasing rate of extinction, and this model is generally rejected as improbable (Benton 2001). The third, density-dependent, model assumes that after an initial slow diversity increase, a rapid rise occurs, followed by a slowing rate of increase and finally a plateau (logistic growth).

In a “decoupled logistic” simulation of the three Phanerozoic evolutionary faunas at the family level, allowing for major mass extinctions, Sepkoski (1981, 1984) achieved a rather good fit to the observed picture. In a variation of the theme, it was proposed that the diversifications from Ordovician to recent were best matched by a series of four simple logistic curves without interaction between evolutionary faunas and only reset by mass extinctions (Courtillot and Gaudemer 1996). Exponential growth (Benton 1995) is currently no more supported for marine animals (Alroy 2010), but the nearly exponential increase in several terrestrial groups indicates that these taxa are still far from reaching saturation (Benton 2001).

Extinctions and Biotic Recovery: Generalities

From the conservation biologist’s point of view, the extinction of even a single species is a catastrophe. From a paleontologist’s viewpoint, species extinction is normal, and more than 99 % of all the species that ever inhabited Earth are now extinct (Raup 1991b). Yet, there is a further, more important dimension to this: during the history of life, mass extinctions also provided huge opportunities for taxa that hitherto had played only minor roles, by removing or marginalizing incumbents (Jablonski 2001).

The same databases used in diversity studies can be used to construct plots of extinction (and also origination) intensities over time. Two major points emerge from such an analysis: peaks of high extinction intensities are separated from each other by times of lesser extinction, and overall extinction intensities decline over the Phanerozoic (Sepkoski 1996; MacLeod 2003, 2013; Fig. 5). According to Raup and Sepkoski (1982), there were 5 major and at least 18 lesser mass extinctions in the Phanerozoic, and the "big five" major extinctions (Table 1) are also recognized in newer studies (Hallam and Wignall 1997; MacLeod 2003, 2013; Bambach et al. 2004; Taylor 2004). A "mass extinction" is an event that (1) was nearly global, (2) removed a significant proportion of the existing species (perhaps more than 30 %), (3) affected species from a broad range of ecologies, and (4) happened within a (geologically speaking) short time.

For the decline in background extinction intensity, widely disparate explanations have been proposed. The change might reflect the general decrease in "volatility" between the three evolutionary faunas (Sepkoski 1981) or secular changes in the geochemistry and nutrition levels in the seas (Martin 1996). Yet, it might also just be a taxonomic artifact: through the Phanerozoic, there is a trend toward more species per family/genus. More species therefore need to become extinct for the entire family/genus to become extinct (Taylor 2004).

An extinction event can be abrupt, or stepped, or gradual. An abrupt or "pulse" extinction evidently leaves a species no time to adapt or migrate, whereas this would be possible during a gradual or "press" extinction (Erwin 1996b, 2001b). Yet, it has proven difficult to establish the exact times of disappearance of taxa, especially the rare ones. As a consequence of the imperfect fossil record, the observed last appearance of fossil taxa is always "smeared back" in time through a time interval before their actual extinction (Hallam and Wignall 1997; Taylor 2004). This "Signor–Lipps effect" (Signor and Lipps 1982) will lead to the perception of a gradual extinction pattern even if it was abrupt. The "zombie" lineage, that is, the unsampled portion of a taxon's range occurring after the final appearance of the taxon in the fossil record prior to its actual extinction (Lane et al. 2005), can be inferred at some level of probability using statistical methods (Marshall 1990).

Not even the largest mass extinctions acted in a completely random manner. Extinction selectivity can be geographical (e.g., tropical versus nontropical, terrestrial versus marine), taxonomic (different extinction rates among higher taxa, e.g., dinosaurs versus mammals, plants versus animals), or linked to trait (e.g., body size, trophic level; McKinney 1997, 2001; Twitchett 2006). The selectivity patterns seen during a major extinction interval can be the same as those acting during pre- and postextinction times ("fair game" selectivity) or they can differ ("wanton" selectivity; Raup 1991b). Random survival with respect to trait and taxonomy was termed "field of bullet" selectivity (Raup 1991b).

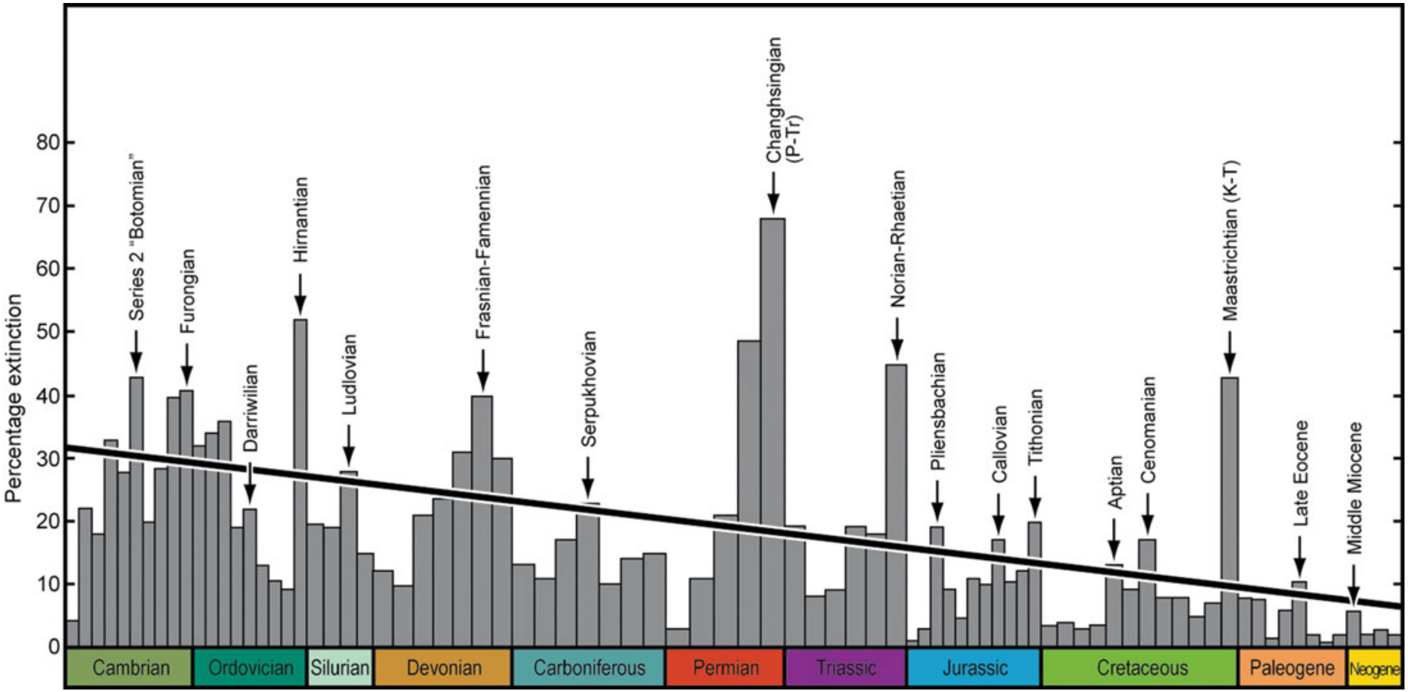

Fig. 5 Extinction intensities in the Phanerozoic. Mass extinctions clearly stand out against background intensities, which decreased during the Phanerozoic (After MacLeod 2003)

Table 1 Observed (families, genera) and calculated (species) extinction intensities at the five major Phanerozoic mass extinctions

Mass extinction	Families extinct (%)	Genera extinct (%)	Species extinct (%)
End Ordovician	26	60	85
Late Devonian	22	57	81
End Permian	51	82	95
End Triassic	22	53	80
End Cretaceous	16	47	73

Simplified after Hallam and Wignall 1997

Major discussion has centered on the question of whether mass extinctions qualify as a separate class of evolutionary mechanism and are, therefore, different from background extinctions (Jablonski 2001; Bambach et al. 2004). There is certainly a continuity of magnitude, with the "big five" and some Early Paleozoic events occupying the ranks of the highest intensities (MacLeod 2003; Wang 2003), although the simple relationship between extinction intensity and mean waiting time (kill curve; Raup 1991a) is no longer accepted because continuity of cause is lacking (Wang 2003; Prothero 2006). The processes operating during mass extinctions are not the same as those acting during background extinctions (Wignall 2004). Continuity of effects is also no longer tenable; for example, the end-Ordovician and end-Devonian mass extinctions both had about the same intensities, but the former had only minor consequences for the structuring of marine communities, while the latter had a profound impact on ecosystems (Droser et al. 2000). Mass extinctions therefore did have a major impact on the evolution of life even though most species have gone extinct during times of background extinction intensities (Taylor 2004).

Did the major mass extinctions during the Phanerozoic have a common cause? This subject was treated by several authors, and the mechanisms include impacts (as assumed, e.g., by Raup and Sepkoski (1984); see review by Racki (2012)), sea-level changes, and the spread of anoxia (Hallam and Wignall 1997; Peters 2008), large-scale volcanisms (Courtillot 1999; Prokoph et al. 2013), and perhaps global cooling (Stanley 1988). It is not always easy to distinguish between the different mechanisms (MacLeod 2003, 2013; Table 2). Yet, there is now overwhelming evidence that the major mass extinctions had their individual signature, and at the present state of knowledge, the search for a common cause no longer makes sense (Prothero 2006; MacLeod 2013).

It has been suggested several times that the history of life follows some large-scale cyclic pattern (Fischer and Arthur 1977; Fischer 1984). Yet, the notion that Phanerozoic extinction patterns show a periodicity with an interval length of 26 Myr (Raup and Sepkoski 1984) has spurred intensive debates about extinction mechanisms. But with increasing accuracy of the geological time scale, it has received little support from other researchers. Currently, few paleontologists would subscribe to the idea that the mass extinctions show any periodicity, despite continued search for possible (mainly extraterrestrial) mechanisms

Table 2 Environmental effects of the most commonly cited mass extinction mechanisms

	Extinction mechanism		
Environmental effect	Comet/asteroid impact	Flood-basalt volcanism	Sea-level change
Increased atmospheric particulates	x	x	x
Increased cloud cover	x	x	
Increased greenhouse gases	x	x	
Reduced greenhouse gases			x
Acid rain	x		
Global wildfires	x		
Shock heating	x		
Habitat fragmentation	x	x	x
Intensification of climate gradients	x	x	x
Enrichment of trace elements		x	

After MacLeod 1998

(e.g., invisible companion of the sun, "nemesis," inducing a comet shower when passing through Oort Cloud; an eccentrical "planet X" doing the same job; the passing of our solar system through the spiral arms of our galaxy, again perturbing bolides in the Oort cloud; movement of the solar system through the galactic plane; Sepkoski 1990). It comes as a major surprise that a new study indicates again that the diversity of life on Earth followed some cyclic pattern, this time with a 62-Myr periodicity (Rohde and Muller 2005). This pattern was recently corroborated (Melott and Bambach 2011a, b); yet statistical support is weak (Melott et al. 2012) and it might just be the inevitable outcome of the applied methods (Smith 2007).

The phase after a mass extinction usually shows a peculiar fauna and flora that change gradually during the time following the extinction. Some terms have proven to be helpful for the characterization of these intervals (Kauffman and Erwin 1995; Fig. 6). The extinction phase is the time where most of the affected taxa had their last appearance. This is followed by the survival phase, where some groups not severely affected by the extinction (holdover taxa) have already began to diversify. During the survival phase, there are usually a small number of opportunistic taxa that could temporarily spread at the expense of the other fauna. "Lazarus taxa" (Jablonski 1986) are those that disappear, probably by becoming very rare (and not retreating to refugia; Wignall and Hallam 1999) during the survival phase, only to later reappear during the recovery phase when new ecosystems are being established, while "Elvis taxa" (Erwin and Droser 1993) are those that have newly entered the fossil record but mimic the shape of extinct taxa. The new communities are largely shaped by progenitor taxa, the most prolific during the recovery phase (Kauffman and Erwin 1995; Hallam and Wignall 1997).

It has long been recognized that after mass extinctions reefs show a prolonged recovery interval. This "reef gap" (Hallam and Wignall 1997; Stanley 2001;

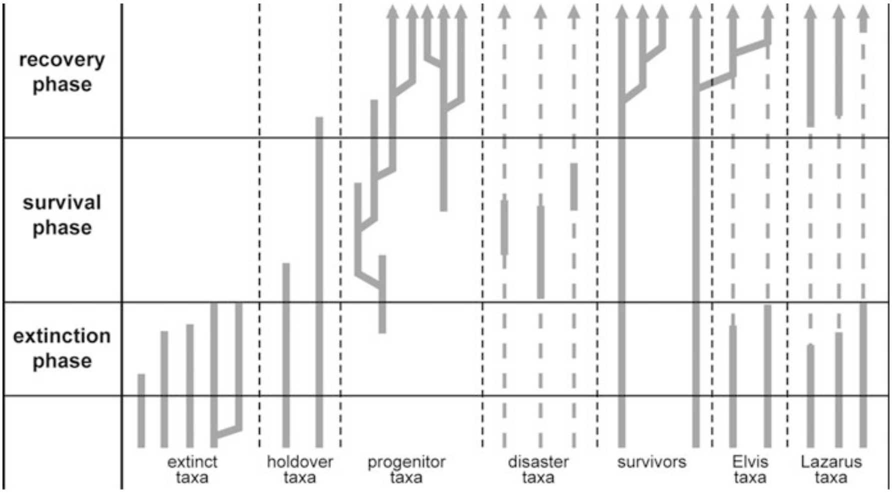

Fig. 6 Faunal patterns during extinctions and subsequent recovery (After Hallam and Wignall 1997)

Flügel and Kiessling 2002; Jablonski 2003), which is evident after all of the "big five" and also after the extinction event after the end of the Lower Cambrian (extinction of the Archaeocyatha; Copper 1988), probably reflects the longer time required to reassemble complex ecosystems (Jablonski 2003).

Selected Case Studies

The Cambrian Explosion and Its Prelude

The tracking of the appearance and early diversification of the animals in the fossil record (Fig. 7) is a rapidly progressing field of paleontology (Fedonkin et al. 2007; Erwin and Valentine 2013). New input has come especially from molecular systematics (Adoutte et al. 2000; Giribet 2002; Pennisi 2003; Halanych 2004; Peterson et al. 2004; Hedges 2009; Edgecombe et al. 2011) and through precise absolute dating of fossiliferous Late Neoproterozoic and Early Cambrian sections, allowing the establishment of a reliable chronostratigraphic framework (Martin et al. 2000; Knoll et al. 2004; Peng et al. 2012).

Possibly the oldest metazoans are ring- and disk-shaped impressions from the Mackenzie Mountains in Northwestern Canada, from the Late Cryogenian Period. This soft-bodied fauna represents perhaps cnidarian grade animals (Erwin 2001a). Considerably more diverse but younger so-called Ediacaran (= Vendian) assemblages are known from a number of localities around the world (Bottjer 2002; Brasier and Antcliffe 2004; Narbonne 2005; McCall 2006). The fauna of these assemblages consists exclusively of soft-bodied forms. The body wall of these organisms must have been quite rigid as is evident from the taphonomic behavior

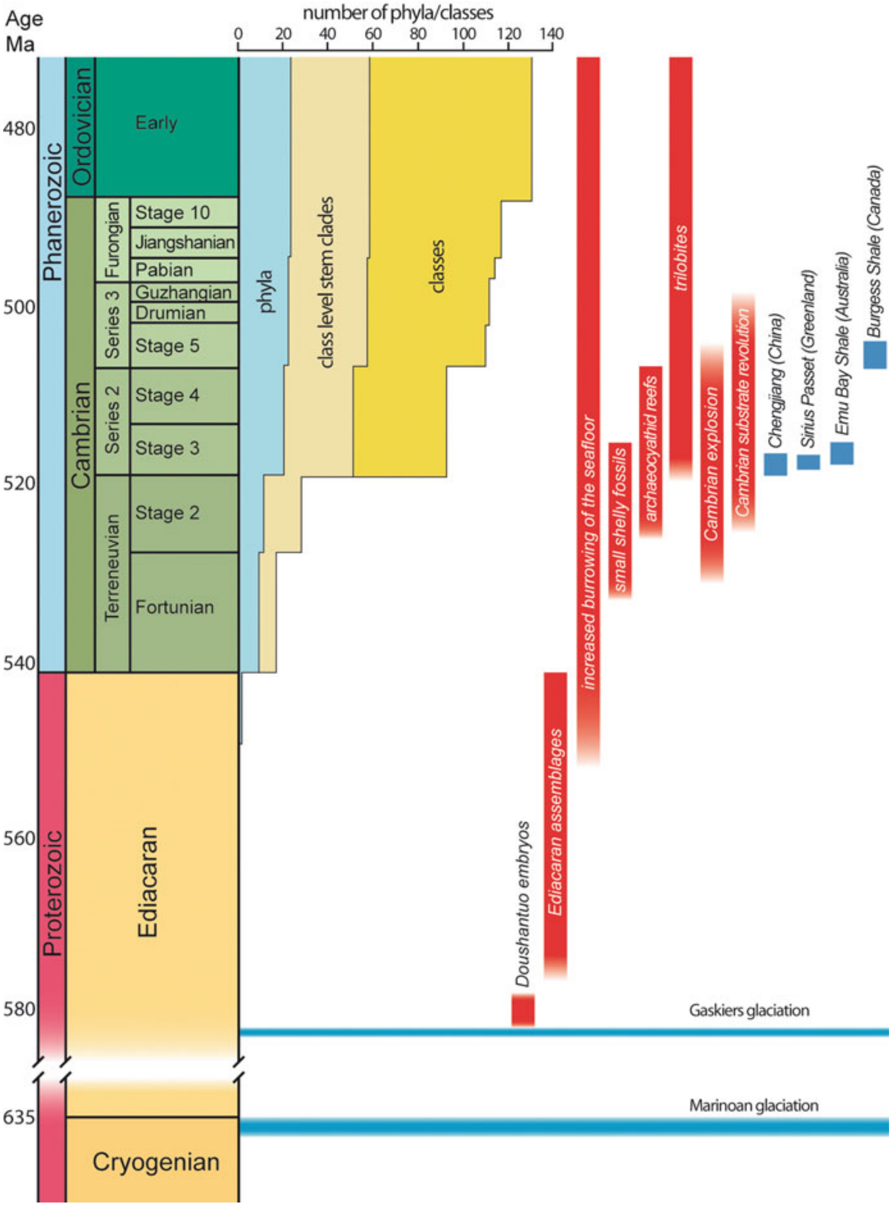

Fig. 7 Major events during the latest Neoproterozoic and the Cambrian (After Erwin and Valentine 2013)

of the Ediacaran biota. They are preserved, mostly intact, as impressions at the base of event beds (storm layers, turbidites) that quickly buried them (Erwin 2001a; Bottjer 2002).

Most of the forms are flattened, segmented, or quilted, and some of them attain considerable sizes (Narbonne and Gehling 2003; Xiao and Laflamme 2009). Classification of these organisms has been highly controversial. Traditionally, the various species were assigned to extant groups like medusae, sea pens, polychaete worms, and stem group echinoderms (Wade 1972a, b; Glaessner 1983, 1984; Jenkins 1992), with most of them belonging to cnidarians. Today most researchers believe that the majority of the enigmatic Ediacaran organisms represent "lost constructions" (Seilacher 1989, 1992; Buss and Seilacher 1994; Narbonne 2004, 2005). With the exception of the 555-Myr-old *Kimberella*, which is now considered to be an ancestral mollusk (Fedonkin and Waggoner 1997; Fedonkin et al. 2007; but see Dzik 2003; Budd and Jensen 2004) and therefore the oldest body fossil of a bilaterian, Ediacaran organisms seem to lack a mouth and a digestive tract. Most were immobile, many of them recliners, but some also mud-stickers (Seilacher 1999). Nutrient uptake was either through the body surface, or these organisms lived in symbiosis with photosynthetic/chemosynthetic protists or bacteria (McMenamin and McMenamin 1990; Narbonne 2005). Still another interpretation of these creatures as lichens (Retallack 2013) is rejected by most paleontologists (e.g., Xiao 2013).

Although sponges and cnidarians were most probably also present, predators were notably absent. The immobile organisms thus lived in a "Garden of Ediacara" (McMenamin and McMenamin 1990). The sediment surface was frequently sealed by microbial mats that were not disrupted by larger burrowing animals. Traces including some radular scratch marks are small and rare and are proof of the presence of bilaterians. Claims for evidence of bilaterians earlier than the Ediacaran assemblages (e.g., traces from 1,200-Myr-old rocks in India; Seilacher et al. 1998) are published with some frequency but are not accepted (Erwin and Davidson 2002; Jensen et al. 2006).

A new window into Late Proterozoic life recently opened with the discovery of 580–560-Myr-old fossiliferous phosphorites at Doushantuo, Southern China (Xiao et al. 1998). In addition to various algae, microscopic multicellular aggregates with preserved nuclei were found. These aggregates were initially described as metazoan embryos (Knoll and Carroll 1999; Valentine et al. 1999; Chen et al. 2000; Hagadorn et al. 2006) but rather seem to be cleavage stages of some unknown "holozoans" or germination stages of protists (Butterfield 2011; Huldtgren et al. 2011). Newer claims for small bilaterian animals (*Vernanimalcula*) with preserved coelom and digestive tract from the same locality (Chen et al. 2004) have been rejected (Stokstad 2004; Bengtson et al. 2012). The Ediacaran biota largely went extinct at the Precambrian–Cambrian boundary (Brasier and Antcliffe 2004; Xiao and Laflamme 2009), with perhaps a few survivors into the Middle Cambrian (Conway Morris 1993; Shu et al. 2006).

The base of the Cambrian, defined by the first occurrence of the trace fossil *Treptichnus pedum* (Buatois and Mangano 2011) and now dated at 541 Myr (Peng et al. 2012), marks the beginning of an interval which is the most remarkable in the history of life. During the Early Cambrian, a wide range of skeleton-bearing animals made their debut, and within only 20 Myr, almost all phyla with preservable hard parts entered the fossil record (sponges already earlier, bryozoans in the Late Cambrian; Valentine 2002, 2004; Marshall 2006; Erwin and Valentine 2013). This apparent explosion of animal bauplans, which had already puzzled Darwin, is still one of the greatest enigmas, although it has become clear in the last few years that there was a prelude of perhaps tens of million years (Lieberman 2003), seen both among traces and in the shelly fossils, but no lengthy time gap between the Ediacaran assemblages and the lowermost Cambrian (Knoll and Carroll 1999; Erwin 2001a; Valentine 2002; Erwin and Valentine 2013).

At first we see an increasing size and complexity of burrows/traces across the Precambrian–Cambrian boundary and then an ever-increasing diversity during the Early Cambrian (Crimes 1992, 2001; Droser and Li 2001; Buatois and Mangano 2011). In parallel, there was a huge diversification in the so-called small shelly fossils (Rozanov and Zhuravlev 1992; Conway-Morris 1998, 2001; Grotzinger et al. 2000). The appearance of new animal phyla and other higher taxa was concentrated in an interval between the Late Terreneuvian and the early Series 2 spanning perhaps 10–20 Myr, and this interval is called the "Cambrian explosion" (Dzik 1993; Valentine et al. 1999; Conway Morris 2000). During this interval, biomineralization was acquired by a multitude of organisms, including mollusks, brachiopods, echinoderms, and chordates (see Lowenstam and Weiner 1989; Bengtson 1994; Zhuravlev and Riding 2001; Wood and Zhuravlev 2012 for an overview). Complex arthropods like trilobite enter the fossil record early in Series 2, and later in Series 2 a plateau in diversity was reached (Marshall 2006; Erwin and Valentine 2013).

Our picture of the Cambrian explosion is facilitated by several wonderful, exceptional fossiliferous settings (Fossil-Lagerstaetten), including the Early Cambrian localities of Chengjiang (China; Xian-guang et al. 2004), Sirius Passet (Greenland; Conway Morris 1998), Emu Bay Shale (Australia; Nedin 1995), and the most famous Middle Cambrian Burgess Shale (Canada; Briggs et al. 1994). Several very important questions surround debates about the Cambrian explosion. (1) Is it real or just an artifact of the imperfect fossil record? (2) Does the origin of metazoan phyla substantially predate their appearance in the fossil record? (3) If the event was real, what was the triggering mechanism?

The current consensus is that the Cambrian explosion was indeed real and happened in just a 10–20-Myr interval in the Late Terreneuvian and early Series 2 (Valentine et al. 1999; Chen et al. 2000; Conway Morris 2000; Marshall 2006; Erwin and Valentine 2013). Yet, the Cambrian explosion does not record the initial split of the metazoans, but rather the diversification at a high taxonomic level (so is therefore, strictly speaking, not a radiation; Erwin and Valentine 2013) of the three fundamental metazoan groups into the crown groups and the modern phyla (Douzery et al. 2004; Peterson et al. 2004; Valentine 2004; Erwin and Valentine 2013). Ecologically, the Cambrian revolution led to a massive restructuring of the marine benthos (Bush and Bambach 2011). An increasing percentage of animals were burrowers that fed on nutrients within the sediment or that constructed tubes. As a consequence of the increasing bioturbation (Droser and Li 2001), the sediment became destabilized, and the superficial microbial mats were lost. This "agronomic revolution" (Seilacher 1999) or "Cambrian substrate revolution"

(Bottjer et al. 2000) led to an uppermost mixed layer, and besides the Ediacara organisms, many immobile recliners and mud-stickers like the helicoplacoid echinoderms went extinct early in the Cambrian (Bottjer et al. 2000; Dornbos and Bottjer 2000; Dornbos et al. 2005).

With respect to the triggering mechanism(s) of the Cambrian explosion, our explanations are still very speculative. The synchronous radiation of many disparate phyla has led strong support to the idea that there must have been an environmental trigger (physical or biological; Valentine 2002, 2004; Marshall 2006; Budd 2008). Among the hypotheses advanced is a significant increase in oxygen in the oceans, but this hypothesis is at odds with observations that oxygen reached sufficient levels to sustain metazoan life long before the Early Cambrian (Knoll 1996; Love et al. 2009; but see Hedges 2004). The amalgamation of continental plates, followed by a transgression, was also cited as a possible trigger (Brasier and Lindsay 2001). There were certainly dramatic changes in the chemistry of the oceans during the latest Precambrian as is evident from isotope studies. Increased nutrient levels in the oceans might have facilitated the radiation (Brasier 1992). Furthermore, a major increase in Ca^{2+} levels is documented during the earliest Cambrian, which certainly facilitated biomineralization (Brennan et al. 2004; Wood and Zhuravlev 2012; Kouchinsky et al. 2012). One of the most commonly involved biological explanations of the radiation is that skeletons developed in a number of groups as an answer to increasing predator pressure (Conway Morris 2001; Porter 2011; see also Stanley 1973) and perhaps also the evolution of animal vision (Parker 2003), thereby allowing new adaptational opportunities. The Cambrian saw the appearance of many carnivores and scavengers, and this trophic group accounted for up to 25 % of the species in the Middle Cambrian (Burzin et al. 2001). Furthermore, the development of planktonic habits in a range of groups greatly increased the complexity of food webs and was also responsible for animal diversification (Butterfield 2001, 2009). In more recent years, the evolution of developmental mechanisms has received much attention. It might well be that key innovations in gene regulation and recombination in early metazoans facilitated the Cambrian explosion (Valentine 2002; Erwin and Valentine 2013).

Many paleontologists were deeply impressed by the wide variety of different body plans, especially among arthropods, that appeared during the Cambrian explosion. The number of taxa known from the famous Cambrian Lagerstaetten that do not fit easily into any classification scheme based on living animals is extraordinary. It was claimed that morphological disparity among Cambrian animals was even higher than that seen today (Gould 1989, 1991) and that some extraordinary evolutionary mechanisms acted during the Cambrian explosion. Measuring morphological disparity is a relatively new field and seems to be a promising avenue to complement measures of taxonomic diversity (Foote 1997; Wills 2001; Erwin 2007). Detailed analyses of arthropods showed that disparity among the Cambrian forms was not higher than among modern species, and the level of appendage specialization is much higher today than in the Cambrian (Briggs et al. 1992; Wills et al. 1994). Special evolutionary processes do not, therefore, seem to have operated during the Cambrian explosion. Yet, it remains nevertheless remarkable how early and synchronous the multitude of higher animal taxa appeared in the fossil record.

The Ordovician Radiation

During the Ordovician, taxic diversity at the family and generic level reached a new maximum which was three to four times that of the Late Cambrian (Miller 1997, 2001). While during the Cambrian explosion numerous phyla and classes representing basic body plans originated, the Ordovician radiation was manifested by an unprecedented burst of diversification at lower taxonomic levels. According to the global picture of Sepkoski (1979, 1997), the Cambrian fauna (e.g., the trilobites) declined, while the articulated brachiopods, the crinoids, stenolemate bryozoans, and other members of the Paleozoic fauna showed a sharp increase. To a lesser degree, members of the Modern fauna like gastropods and bivalves also diversified (Miller 2001, 2012; Servais et al. 2009, 2010).

The almost exponential increase in diversity was much more rapid during this Great Ordovician Biodiversification Event (GOBE) than at any other time of the Phanerozoic (Sepkoski 1997; Webby 2004; Servais et al. 2009). This global diversity increase seems to have been the combined result of an increase in α- (within community), β- (between communities), and γ-diversity (biogeographical differentiation between faunal provinces; Webby 2004). New ecological guilds appeared, and the spatial organization of the benthic communities became considerably more complex (Bottjer and Ausich 1986; Droser and Bottjer 1989, 1993; Servais et al. 2009, 2010). The Ordovician was also a time of marked shift in the reef biota. Whereas Early Ordovician reefs were mainly built of microbial mats and stromatolites, large metazoan-dominated framework reefs had developed and spread on all continents by the end of the Ordovician (Webby 2004; Adachi et al. 2011). The diversification and spread of metazoan reefs was accompanied by an increase in bioeroding organisms colonizing reefs and hardgrounds (“bioerosion revolution”; Wilson and Palmer 2001).

Yet, when the global picture is dissected at finer taxonomic, geographical, and environmental levels, some surprising results emerge (Miller 1997). The diversification seems not to follow a global trajectory but to respond much more to local conditions in paleogeography, sedimentary environment, and orogenic activity. The general decline of Sepkoski’s Cambrian fauna is an oversimplification. The “smooth” global diversity increase during the Ordovician is thus the aggregate record of many regional patterns which were for the most part abrupt (Miller 1997, 2001, 2004, 2012; Westrop and Adrain 1998).

Not a single reason, but rather a combination of paleogeographic, sedimentologic, geochemical, and perhaps intrinsic factors, seems to have been responsible for diversity increase during the Ordovician (Harper 2006a; Miller 2012). The paleogeographic situation was one of a highly fractured continental crust with many small continents. Together with a very high sea-level stand and

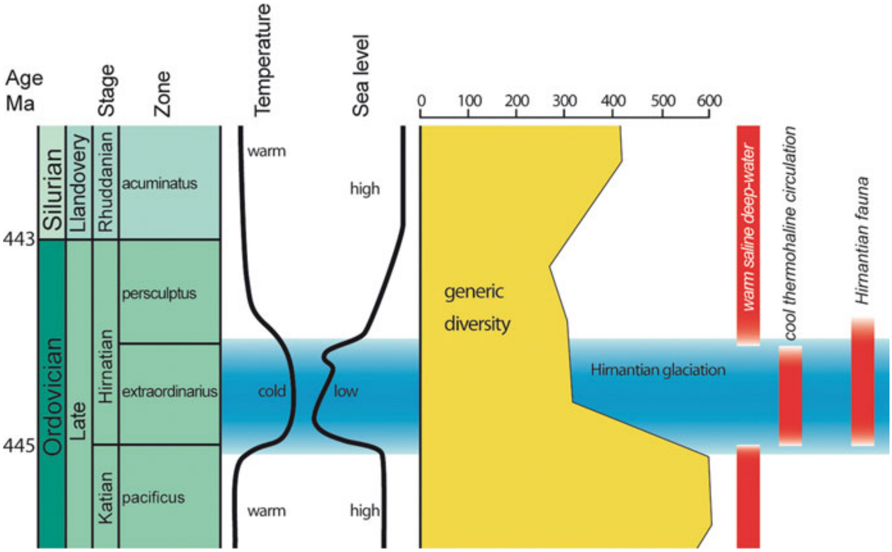

Fig. 8 Major events during the Late Ordovician mass extinction (Modified after Brenchley 2001)

increasing nutrient inputs, this provided extensive shelf areas in many different parts of the world and, therefore, a multitude of colonizable areas (Miller 1997). There is also a good correlation between diversity increase and orogenic activity. Throughout the Ordovician and the remainder of the Paleozoic, there was clearly a trend toward increased primary productivity and away from oligotrophic conditions (Martin 1996). Whether climate change (Trotter et al. 2008) and a series of impacts (Schmitz et al. 2008) also promoted the diversity increase remains to be scrutinized.

The Late Ordovician Mass Extinction

With 26 % of the marine families, up to 60 % of the genera and an estimated 85 % of all the species becoming extinct, the Late Ordovician mass extinction was one of the most severe extinction episodes in the Phanerozoic, surpassed in its magnitude only by the end-Permian mass extinction. Its extent was global, and it affected nearly all benthic and pelagic groups (Hallam and Wignall 1997; Brenchley 2001; Sheehan 2001b; Rasmussen and Harper 2011; Fig. 8).

During the Late Ordovician greenhouse conditions prevailed. But during the latest stage (Hirnantian), a short glaciation of approximately 0.5-Myr duration occurred (Brenchley 2001; Sheehan and Harris 2004; Delabroye and Vecoli 2010). The glaciation probably started when Late Ordovician orogenic activities led to extensive exposure and weathering of silicate terrains and, therefore, CO_2 consumption. Under falling CO_2 levels, ice sheets started to grow and albedo feedback led to an extensive Gondwana glaciation. The ice cover in turn inhibited silicate weathering, and CO_2 levels rose again. After a threshold was reached, greenhouse conditions returned and the ice caps melted quickly (Kump et al. 1999). It is now well documented that the mass extinction during the Late Ordovician was a two-phase event, and the first extinction pulse at the base of the Hirnantian *extraordinarius* zone corresponded to the initiation of the Gondwana glaciation and the second pulse in the first third of the *persculptus* zone to the rapid decay of the polar ice cap.

During the first extinction event, various groups suffered heavy losses, and the graptolites nearly died out. Thereafter, an impoverished and remarkably cosmopolitan benthic fauna was present on most shelves from high latitudes to the tropics. This so-called Hirnantia fauna can be regarded as a cool-adapted, opportunistic community that spread after the extinction removed the hitherto dominant species (Brenchley 2001; Sheehan 2001b; Jia-Yu et al. 2002). Primary productivity was obviously much reduced during the Hirnantian.

The second extinction phase was again sharp and hit most of the groups that had already suffered during the first extinction pulse. It eliminated much of the benthic Hirnantia fauna, but the recovery interval did not last very long. It is most surprising that the faunal turnover during the Late Ordovician mass extinction was accompanied by very little ecological change and the structure of Silurian communities is remarkably similar to those of the Late Ordovician (Droser et al. 2000; Bottjer et al. 2001; Sheehan 2001b; McGhee et al. 2004).

The causes of the two extinction pulses were certainly linked to the rapid onset and the later abrupt termination of the Gondwana glaciation during an otherwise warm climatic mode (Fortey and Cocks 2005; Delabroye and Vecoli 2010). Responsible for the necessary lowering of the atmospheric CO_2 was perhaps the expansion of the first land plants (Lenton et al. 2012). Global cooling of the oceans of perhaps as much as 8 °C together with a loss of benthic habitat due to regression might have, in part, been responsible for the first extinction (Berry and Boucot 1973; Brenchley et al. 1994; Armstrong 1996). Yet, pelagic forms also suffered heavy losses, and changing circulation patterns in the oceans were probably crucial (Hallam and Wignall 1997). The widespread deep anoxic waters, the extensive dysoxic zone, and the nutrient-rich surface waters vanished during the onset of the glaciation when cold, deep water led to intensified ocean circulation. During the second pulse, the termination of cold, deep water production led again to widespread stratified oceans with anoxic deep and intermediate dysoxic waters. Black shales accumulated again, and the transgressing dysoxic waters eliminated most of the benthic Hirnantia fauna and other benthic organisms not resistant to oxygen-poor conditions (Hallam and Wignall 1997; Rasmussen and Harper 2011).

The Late Devonian Biodiversity Crisis

Between 11 and 16 global events have been identified in the Givetian through Famennian stages (Walliser 1996; Becker et al. 2012), but only the lower and upper

Kellwasser events (Frasnian–Famennian boundary) and the Hangenberg event (uppermost Famennian) are of a magnitude that would deserve the name mass extinction (Hallam and Wignall 1997). Yet, the stress imposed by the many smaller events, especially the earlier Taghanic event in the Late Givetian (Aboussalam and Becker 2011; Zambito et al. 2012), was probably crucial for the overall extinction patterns in maintaining a high level of environmental stress throughout the Late Devonian. The label "mass extinction" is somewhat misleading as it was rather an anomalously low speciation rate that was responsible for the drop in biodiversity (Bambach et al. 2004; Stigall 2012).

At least 70 % and perhaps as many as 82 % of the marine species vanished during this time period (McGhee 1996, 2001; Fig. 9). Among the groups that were most severely hit were the reef builders (Fagerstrom 1994; Hallam and Wignall 1997; Copper and Scotese 2003), but other benthic organisms, especially tropical families, also suffered heavy losses during both major crises. The toll was no less severe in planktonic and nektonic groups (Racki 2005), and the armored agnathans and the placoderms went completely extinct (Hallam and Wignall 1997).

Quite important for the elucidation of the possible causes of the Late Devonian mass extinctions is that their selectivity differed between the different events. The Taghanic event affected mainly benthic taxa from low-latitude, shallow-water environments (Hallam and Wignall 1997). The Kellwasser events also affected mainly warm-water species as well as planktonic and pelagic groups. During the Hangenberg crisis, it was the planktonic and nektonic groups that were most severely hit, while the benthic groups showed a better survival than at the Frasnian–Famennian boundary.

The extinction patterns in the Late Devonian were highly complex and a result of several mechanisms spread over a time period of more than 10 Myr, with the most severe perturbations concentrated at the Frasnian–Famennian boundary and in the latest Famennian (Sandberg et al. 2002; Stigall 2012). Global cooling of the oceans (Copper 1986) was certainly one of the main causes of the extinctions (McGhee 1996, 2001; Brezinski et al. 2009), although the Gondwana glaciation only started in the Late Famennian (Caputo 1985; Algeo and Scheckler 1998). Yet, besides the cooling, frequent sea-level changes including both eustatic rises associated with spreading anoxic waters and regressions responsible for habitat loss are also well documented (Sandberg et al. 2002; Ver Straeten et al. 2011). The Late Devonian was also a time of increased impact frequency. Well-dated craters, shocked minerals, and microtektites as well as iridium anomalies are known from different continents (McGhee 1996, 2001; Sandberg et al. 2002), and these impacts probably increased the environmental stress.

Devonian to Carboniferous Expansion of Land Flora

Undisputed vascular land plants are known from Late Silurian strata, but spores occur already in the Middle Ordovician (Taylor et al. 2009; Kenrick et al. 2012).

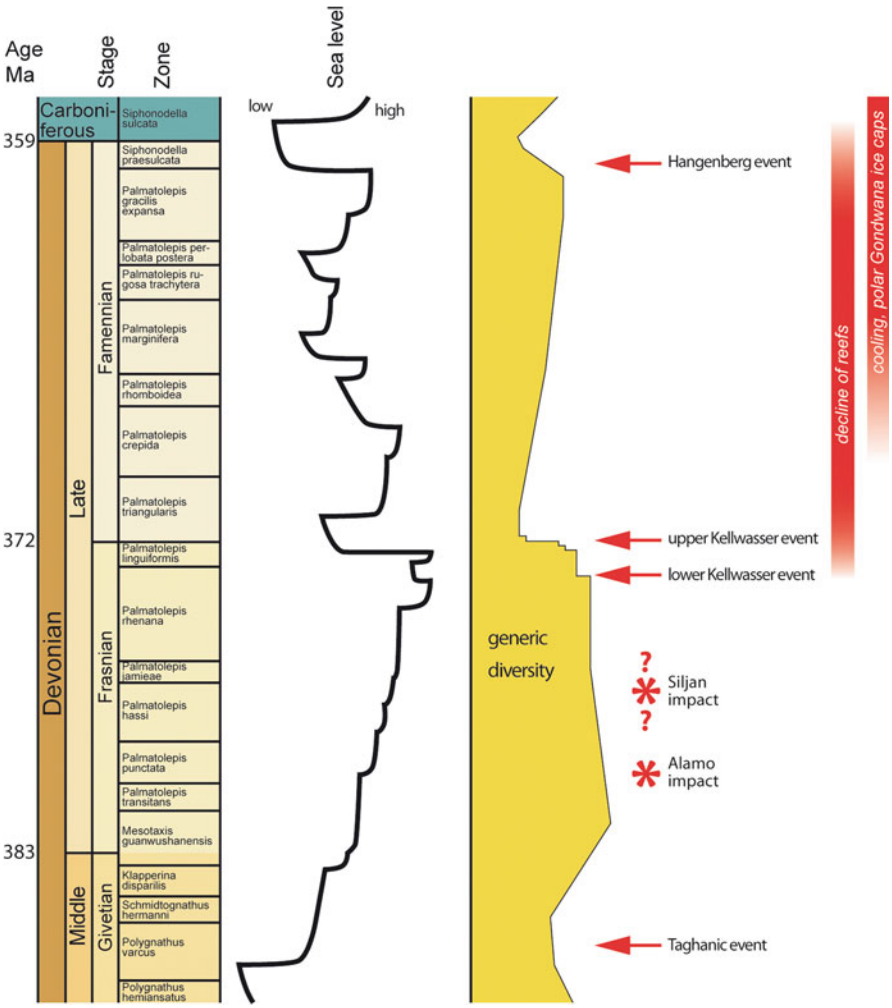

Fig. 9 Major events during the Late Devonian mass extinction (Modified after various sources)

Colonization of the terrestrial environment, at least in moist lowlands, obviously happened rather quickly, and within only 45 Myr, all major land-plant lineages and organizational grades (except for flowering plants) developed (Niklas 1997, 2004; Willis and McElwain 2002; Taylor et al. 2009). All the morphological adaptations including a protective outer covering (waxy cuticula) against desiccation, stomata to allow gas diffusion, specialized tissues for the transport of liquids, and rigid cell walls (Chaloner 2003) developed in the Devonian, although accompanied only by a modest diversification at the species level (Niklas 1997; Willis and McElwain 2002). By the end of the Devonian, the terrestrial environment saw the first globally distributed forests with large trees (Chaloner 2003; Taylor et al. 2009).

This resulted in a huge increase in biomass that culminated in the Late Carboniferous. Much of this organic material was not decomposed and recycled, but instead buried in moist anoxic soils (acidic swamps; Chaloner 2003).

This expansion of the land flora had a profound impact on Earth's environmental conditions. Most important was the removal of large quantities of CO_2 from the atmosphere through photosynthetic carbon fixation. The most widely accepted models for Phanerozoic CO_2 show a sharp decrease from about 15 times the present level (15 PAL) at the beginning of the Devonian to 10 PAL at the Devonian–Carboniferous boundary and a further decrease to less than 2 PAL in the Late Carboniferous (Berner 1998; Royer et al. 2000). With the massive drop in available CO_2, a high stomatal density became crucial, and the laminate leaf rapidly became widespread (Beerling et al. 2001) although at the cost of higher water loss through transpiration (Chaloner 2003; Taylor et al. 2009).

During the Devonian, an increase in the sizes of the trees was accompanied by increasing depth and complexity of the roots (Algeo and Scheckler 1998). This in turn accelerated silicate weathering and led to a further drawdown of carbon as bicarbonate into rivers and ultimately into the seas (Kump et al. 2004). The most obvious consequence of this huge decrease in atmospheric CO_2 was the onset of the Gondwana glaciation. In the Late Devonian, the southern continents were assembled near the South Pole, and the first polar ice caps developed in the latest Devonian. However, the main phase of the Late Paleozoic glaciation started in the Early Carboniferous. With its duration of more than 80 Myr (Crowley and North 1991; Frakes et al. 1992; Vaughan 2007), well into the Permian, this glaciation was by far the longest and also the latitudinally most extensive of the Phanerozoic ice ages. Yet, it was not associated with any major mass extinction pulse.

The very high productivity of the plants during the Devonian and Carboniferous also led to a significant increase in atmospheric oxygen, with 30–38 % O_2 in the Late Carboniferous (Berner 1999; Berner et al. 2003; Bergman et al. 2004). This seems to have had yet another impact on life. With increasing oxygen partial pressure, the diffusive flux is increased considerably, allowing the evolution of gigantic sizes (Graham et al. 1995; Dudley 1998), most notably among fish, terrestrial arthropods, and amphibians (Briggs 1985; Graham et al. 1995; Dahl et al. 2010; Harrison et al. 2010). For the giant flying insects, the higher density of the atmosphere might also have played a role (Dudley 1998, 2000).

The End-Permian Mass Extinction and Subsequent Recovery

The mass extinction at the end of the Permian has long been recognized as the most severe of all the Phanerozoic perturbations (Phillips 1860). The radical faunal change associated with this biotic crisis was the reason for distinguishing between the Paleozoic below and the Mesozoic above. More than 50 % of marine and terrestrial families went extinct and an estimated 80–96 % of all the species. Until recently (Erwin 1990, 1993), the end-Permian mass extinction was seen as a protracted crisis, which lasted for approximately 10 Myr. Newer research has

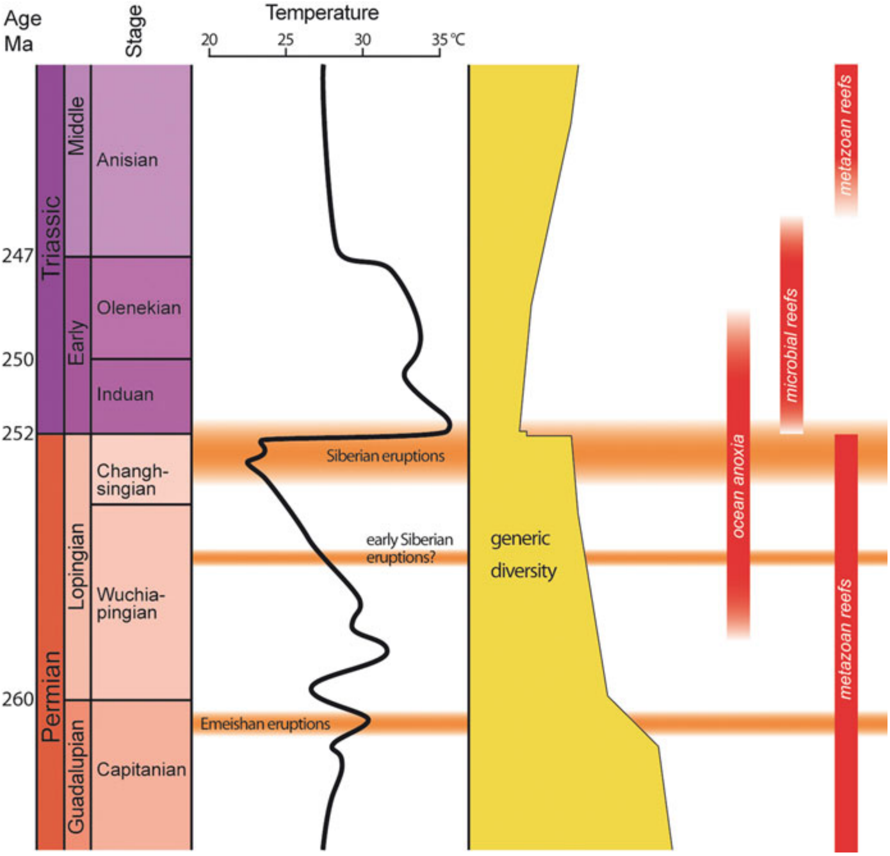

Fig. 10 Major events during the end-Permian mass extinction (Modified mainly after Chen and Benton 2012; Sun et al. 2012)

shown that there were actually two discrete events (Fig. 10). The first occurred in the latest Guadalupian (terminal Middle Permian) and affected only some groups in a more gradual way (Hallam and Wignall 1997; Clapham et al. 2009). The event at the very end of the Permian, and reaching slightly into the lowermost Triassic, was apparently of quite short duration (probably less than 0.2 Myr; Erwin et al. 2002; Shen et al. 2011). It is this interval that has been called "the mother of all extinctions," "the great dying," or the "Paleozoic nemesis" (Erwin 1996a, 2006; Benton 2003). This massive crisis affected all groups of organisms, both in the seas and on land (Benton and Twitchett 2003; Algeo et al. 2011).

In the Middle Permian, the seas were teeming with life, and many different faunal provinces can be distinguished. Highly diverse stromatoporoid–coral reefs were widely distributed. On soft and hard bottoms, rich communities dominated by brachiopods and echinoderms flourished, and in the water column, numerous ammonoids and various fish groups had attained a high diversity. On land, insects had reached their highest diversity in the Paleozoic, and tetrapod communities were probably as complex as modern mammal communities (Benton 2003; Sahney and Benton 2008). Plants were also highly diverse and distributed in different biogeographical provinces.

During the first extinction event, which occurred at the end of the Middle Permian (Guadalupian), some groups were affected both on land and in the seas, but none became entirely extinct (Hallam and Wignall 1997; Algeo et al. 2011). The reasons for this first extinction pulse are not well understood, but global cooling, loss of habitat area, and spread of anoxic waters have been cited as underlying causes (Stanley 1988; Hallam and Wignall 1997; Clapham et al. 2009).

The second, and by far the more severe, extinction pulse near the Permian–Triassic (P–Tr) boundary affected all the taxonomic and ecological groups, both in the seas and in the terrestrial environment. Among the larger groups that went completely extinct in the seas were the rugose and tabulate corals, fenestrate bryozoans, and orthid brachiopods. On land, glossopterids and cordaitales were suddenly replaced by a low-diversity conifer–lycopod–fern assemblage with little provinciality. Palynological samples from immediately above the P–Tr boundary are dominated by fungal spores which normally account for only a small proportion of the pollen and spores. This “fungal spike” (Eshet et al. 1995; Visscher et al. 1996; some fungal spores might rather be freshwater algae; see Wignall 2008) was similar in its magnitude to the “fern spike” at the Cretaceous–Tertiary boundary and might indicate vast areas of rotting plants which were decomposed by fungi (Hallam and Wignall 1997; Benton and Twitchett 2003). A wide range of tetrapods, among them the hitherto dominant pareiasaurs, went abruptly extinct, and the Early Triassic vertebrate faunas were completely dominated by the single genus *Lystrosaurus* (Hallam and Wignall 1997; Benton and Twitchett 2003; Ward et al. 2005; Sahney and Benton 2008). Both the magnitude (up to an estimated 96 % of the marine species) and the extraordinary long recovery interval were remarkable. It took almost 100 Myr for family diversity to reach preextinction levels and almost 10 Myr for complex ecosystems like reefs to become established again (Benton and Twitchett 2003; Erwin 2006). The first communities that appeared during the recovery interval are composed of a remarkably cosmopolitan, opportunistic fauna of thin-shelled bivalves (e.g., *Claraia*) and lingulid brachiopods (Hallam and Wignall 1997). Burrowing organisms were almost completely absent, and disaster taxa like stromatolites became locally abundant (Schubert and Bottjer 1992). Lazarus taxa were especially common among the gastropods, and most of them were small (“Lilliput” effect; Twitchett 2006). The long-term consequences for seafloor communities were the replacement of the hitherto dominant epibenthic sessile suspension feeders by a vagile, epi- and endobenthic, mollusk-dominated fauna (Hallam and Wignall 1997; Algeo et al. 2011; Campi 2012). The recovery interval after the end-Permian mass extinction was longer than for any other extinction event (although not for all groups, e.g., ammonites; Brayard et al. 2009), indicating that the ecosystems were almost completely devastated and severe environmental perturbations continued through the Lower Triassic (Twitchett 1999; Payne et al. 2004; Chen and Benton 2012).

The scenario for this mass extinction and its likely causes has received much attention in the last decade. All the evidence indicates that the mass extinction event lasted less than 200 kyr and occurred during a phase of marine transgression and severe global warming (Shen et al. 2011). The catastrophe probably started with the release of huge amounts of CO_2 into the atmosphere, first through volcanic eruptions in South China (Emeishan flood-basalt province; Lo et al. 2002) and perhaps also through coal oxidation (Hallam and Wignall 1997), later through vast eruptions in Siberia (Siberian traps; Courtillot 1999; Wignall 2001a; Benton and Twitchett 2003; Heydari et al. 2008). This led to global warming and in the seas to decreased ocean circulation and oxygen depletion (Wignall and Twitchett 1996), perhaps concentrated in the later part of the extinction event (Song et al. 2013). With further increasing CO_2 levels, methane hydrates began to melt and released large quantities of methane, which first acted as greenhouse gas and later was oxidized to CO_2. Through this positive feedback, a "runaway greenhouse" developed, which went out of control after some threshold was reached (Benton and Twitchett 2003). The seas flooding the shelves became hot, anoxic, and perhaps even sulfidic (Kump et al. 2005; Sun et al. 2012) and killed most of the benthic and pelagic organisms (Clapham and Payne 2011; Payne and Clapham 2012). Ocean acidification was especially deleterious for heavily calcified taxa (Knoll 2013). On land, the vegetation suffered a severe deterioration with equally devastating consequences for the animals, which perhaps also experienced hypoxic stress (Huey and Ward 2005).

Inevitably, many additional or alternative explanations have been presented. A major global regression during the terminal Permian was long a popular explanation for the extinction, but this is no longer tenable. There was clearly a transgression during the P–Tr boundary interval (Hallam and Wignall 1997). Darkening and global cooling with a collapse in photosynthesis was also proposed as extinction cause (Campbell et al. 1992), but all the evidence points to global warming at the end of the Permian. Older suggestions include brackish oceans and an increase in cosmic radiation. The claim for evidence of an impact is relatively recent (Becker et al. 2001, 2004; Frese et al. 2009). However, the impact hypothesis has not received much support (Erwin 2003, 2006). The end-Permian mass extinction thus seems truly "homemade" (White 2002; Benton and Twitchett 2003; Erwin 2006; Payne and Clapham 2012).

End-Triassic Extinction

The extinction at the end of the Triassic (Fig. 11) is recognized as one of the "big five" Phanerozoic mass extinctions, but documenting the exact timing and the causes of biotic overturn has proven difficult. There was a widespread regression at the end of the Triassic, and marine sections which span the Triassic–Jurassic (Tr–J) boundary are known from only a few localities (Hallam and Wignall 1999; Ogg and Hinov 2012a).

Many marine groups suffered a dramatic and sudden decrease in diversity at the end of the Rhaetian, but others witnessed a major reduction in diversity already at

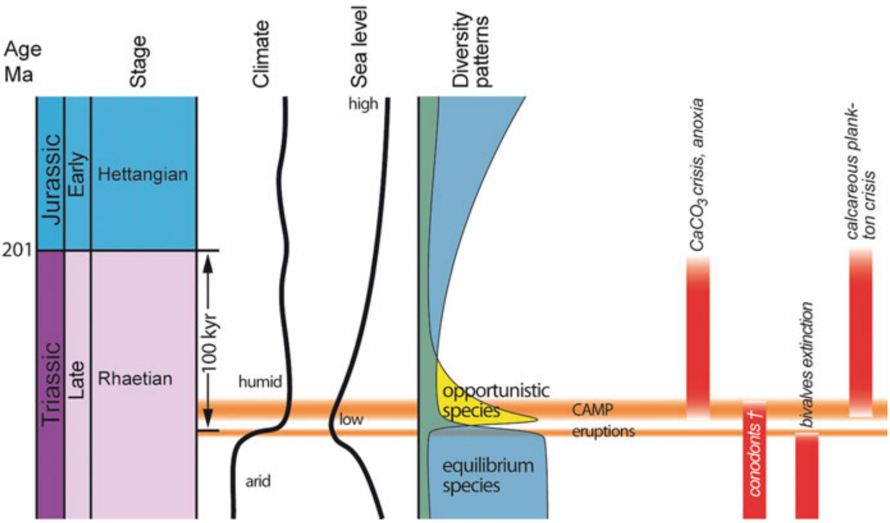

Fig. 11 Major events during the Late Triassic mass extinction (Modified after McRoberts et al. 2012)

the Carnian–Norian boundary and during the Early Rhaetian (Teichert 1990; Hallam 2002; Tanner et al. 2004; Wignall and Bond 2008). Terrestrial plant extinctions are concentrated around the Carnian–Norian boundary and at the Tr–J boundary (Deenen et al. 2010), and the latter boundary layer contains an unusually high fern spores/pollen ratio (Olsen et al. 1990, 2002). Among terrestrial vertebrates, a major extinction is undisputed, but the main turnover occurred near the Carnian–Norian boundary (Benton 1994; Lucas 1994).

Habitat loss and changing substrates associated with the regression in the Late Rhaetian, followed shortly thereafter by a transgression at the Rhaetian–Hettangian boundary, together with shallow water anoxia and perhaps ocean acidification (Greene et al. 2012; McRoberts et al. 2012), were responsible for the observed pattern in the marine realm.

The two extinction phases correspond to two pulses of flood-basalt volcanism (Deenen et al. 2010). This extensive and widespread volcanism related to the rifting of Pangaea around the North Atlantic at the Tr–J boundary was only recently recognized. The outgassing of CO_2 from this Central Atlantic Magmatic Province (CAMP; Marzoli et al. 1999; Wignall 2001a) might have had truly deleterious effects like enhanced seasonal fluctuations and an increase in the number and severity of hot days as well as a decrease in ocean water oxygenation (Huynh and Poulsen 2004). Extreme greenhouse warming, perhaps combined with the release of toxic gases, also explains the extinction patterns on land (Deenen et al. 2010).

An impact scenario (Olsen et al. 2002) is largely dismissed today because the extinction pattern is not a sudden, catastrophic one, various impact craters have been dated as Carnian–Norian, and claims for significant iridium anomalies and shocked quartz could not be verified (Hallam 2002; Tanner et al. 2004).

Mesozoic Marine Revolution

The term "Mesozoic marine revolution" (MMR) (Vermeij 1977) refers to the idea that during the Mesozoic, a profound reorganization in the marine communities led to a significant increase in predation pressure and prey species developed various adaptations (thicker shells, spines, behavioral responses) to cope with this increasing pressure ("arms race" or "escalation"; Vermeij 1987; Harper 2003, 2006b). It is undisputed that during the Mesozoic, especially during the Jurassic and Cretaceous, the number of marine grazers as well as durophagous and drilling predators increased considerably (Vermeij 1977, 1987, 2004; Bambach et al. 2007; Finnegan et al. 2011).

This rise in predatory groups was accompanied by profound changes in marine benthic communities. The epifaunal guilds, like stalked crinoids and brachiopods, that were so characteristic of Paleozoic communities vanished from shallow-shelf environments, and those epifaunal species that did persist in shallow water show a high frequency of regeneration and, therefore, of predator attacks (Vermeij 1987). A marked shift toward infaunal life modes is documented in post-Paleozoic echinoids, gastropods, and especially bivalves (Stanley 1977; Thayer 1983; Vermeij 1987), although this shift predates the appearance of most shell crushers (Harper 2003, 2006). The most conspicuous changes during the MMR occurred in shell architecture. Overall, the shells became sturdier, more highly armored, and developed spines, ribs, and thickened and narrowed apertures (Vermeij 1977, 1987, 2004; Ward 1981, 1983). At least among gastropods, shell-repair scars became much more frequent, pointing again to increasing predation pressure.

According to Vermeij (1987), it was the biological interactions (competition, predator–prey relations) that led to the evolution of these long-term trends. Yet, the biological evolution toward increasing predator-resistant shells might also have been facilitated by changes in the abiotic conditions. Extensive volcanism, which in turn augmented water temperature, high nutrient levels, and a high sea-level stand, facilitated the production of energetically expensive massive shells (Vermeij 1995) and perhaps as well the general increase in diversity and increasing "fleshiness" of the fauna throughout the Mesozoic and Cenozoic (Bambach 1993; Bambach et al. 2007; Bush et al. 2007). For several groups, the timing of changes does not support biological interactions as driving forces (Harper 2003, 2006; Madin et al. 2006; Baumiller et al. 2010; Kosnik et al. 2011).

Secular changes in oceanographic and geochemical conditions most certainly spurred other important changes in the marine biota during Middle and Late Mesozoic times. Planktonic foraminifers appeared in the Middle Jurassic and became numerically important during the Cretaceous. Coccoliths are known since the Triassic, but they became widespread and abundant during the Late Jurassic and the Cretaceous (Ogg and Hinov 2012a, b). This rise in planktonic calcifiers was perhaps facilitated by the intensified bioturbation of the seafloor which effectively recycled nutrients (Kelley and Hansen 2001), but had in turn tremendous effects on the carbon cycle and the $CaCO_3$ saturation of the oceans (Ridgwell 2005).

End-Cretaceous Mass Extinction

This is certainly the most widely known and probably also the best investigated of the major mass extinctions, simply because the popular (nonavian) dinosaurs disappeared at the Cretaceous–Paleogene (K–Pg) boundary (formerly known as the K–T boundary, but the Tertiary is no longer a formal unit of the revised time scale). Yet, it is, with a 16 % loss of the families, a 47 % loss of the genera, and an estimated loss of at least 70 % of the species in the marine realm, the least severe among the five major mass extinctions in Earth history (Jablonski 1994; Hallam and Wignall 1997; Fig. 12). Some marine groups disappeared completely at the end of the Cretaceous (e.g., ammonites, large marine reptiles), others suffered heavy losses (especially planktonic groups), but there were also groups that exhibited little or no reduction over the last Cretaceous to the lowermost Paleogene (MacLeod et al. 1997; Norris 2001; MacLeod 2013).

On land, plants suffered a sharp decrease in diversity that was previously underestimated (Nichols and Johnson 2008), and in many sections a short proliferation of ferns at the expense of angiosperms ("fern spike") is documented. Among the tetrapods, amphibians, turtles, crocodilians, and eutherian mammals were only mildly affected by the K–Pg boundary event, whereas lizards and marsupials suffered heavy losses (Archibald and Fastovsky 2004; Longrich et al. 2012). Primates had their origin in the Late Cretaceous (Chatterjee et al. 2009; Steiper and Young 2009). Yet, because the oldest primate fossils date from the Paleocene (Williams et al. 2010), it is unknown whether this group experienced losses during the K–Pg extinction. For the ornithischians and the (nonavian) saurischians, this

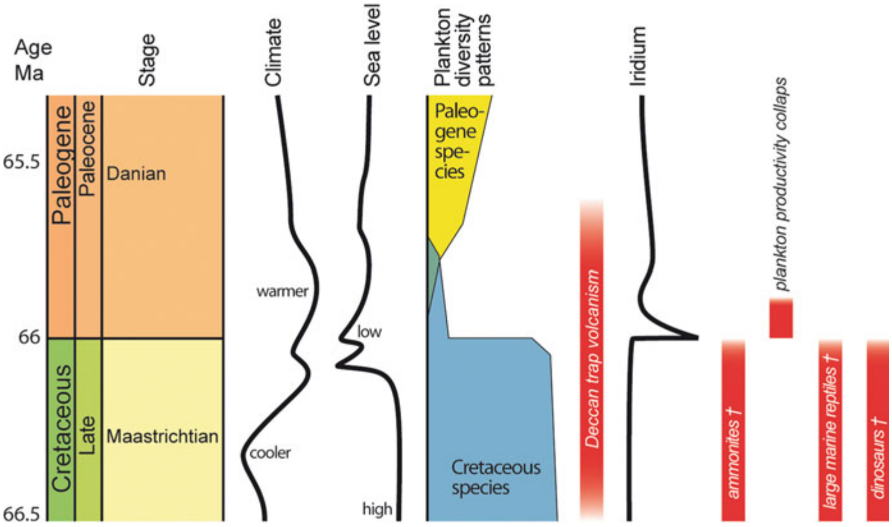

Fig. 12 Extinction patterns during the K–T mass extinction (Modified mainly after Schulte et al. 2010)

event was of course the end of a long era. Land-dwelling species were more severely hit than freshwater inhabitants, endothermic tetrapods (including ornithischians and saurischians) more than ectothermic, and larger more than smaller species (Archibald 1996, 2011; Archibald and Fastovsky 2004).

Evidence for both a gradual decline in dinosaur species richness as well as for a catastrophic and (geologically spoken) instantaneous extinction of the dinosaurs has been presented (Hurlbert and Archibald 1995; Archibald and Fastovsky 2004; see review in Brusatte 2012), but recent data indicate that there was no gradual decline in dinosaur diversity in the latest Cretaceous (Upchurch et al. 2011). The picture is equally complicated in marine exposures in which again evidence for both a gradual as well as a sudden extinction was presented (see MacLeod et al. 1997; D'Hondt 2005). Yet, resampling of formerly investigated sections extended taxonomic ranges upward, and the reported gradual decline of many groups might well be a consequence of the Signor–Lipps effect (Ward 1990).

Among the possible causes for the K–Pg mass extinction that are still considered today are volcanism, climatic fluctuations, and marine regression and an asteroid impact (Benton 1990; Archibald 2011; MacLeod 2013). There is indeed overwhelming evidence that the Earth was hit by a major asteroid perhaps 10 km in diameter that had a devastating impact on Earth's life. This evidence includes molten sediment particles (glass spherules), shocked quartz grains, and a worldwide recognized enrichment in iridium in K–Pg boundary layers (Alvarez et al. 1980, 1995). The impact hypothesis received further support with the discovery of a 66-Myr-old impact crater (Chicxulub) on the Yucatan peninsula, Mexico (Hildebrand et al. 1991). Yet, it has also been demonstrated that the latest Cretaceous was a time of major climatic fluctuations (Skelton 2003) and the pronounced marine regression at the end of the Maastrichtian has been recognized for a long time. In addition, intensive volcanism, which spanned less than 2 Myr over the K–Pg boundary, is documented from the so-called Deccan Traps (Courtillot 1990, 1999). These represent immense outpourings of lava in what is today India and must have had a profound impact on the biosphere (Kelley 2003).

Currently, there are two schools of thought to explain the K–Pg mass extinction. According to the gradualistic, multiple-causes scenario (Archibald 1996, 2011; Archibald and Fastovsky 2004; MacLeod 2013), the climatic fluctuations and the marine regression near the end of the Cretaceous profoundly changed the available habitats in both the terrestrial and marine environments. This biotic stress led to a gradual decline in the dinosaurs and other terrestrial vertebrates. Likewise, the regression also imposed a major stress on the marine animals by reducing the available shelf environments. Further stress was imposed by the Deccan Trap volcanism that erupted large amounts of dust into the atmosphere, with general cooling of the globe, drying of many terrestrial ecosystems, and slowing of the photosynthetic activity as the most likely consequences.

The asteroid impact at the K–Pg boundary is not disputed by most in the gradualist camp, but is seen merely as a moderate "last strike" that led to the collapse of already weakened ecosystems and extinguished animal groups that were already in decline (MacLeod 2013). Only a few researchers deny that the

Chicxulub impact played a crucial role in the K–Pg extinction. These maintain that the impact either postdated (Hildebrand et al. 1991) or predated (Keller et al. 2003; Keller and Adatte 2011; Keller 2012) the K–Pg boundary by several hundred thousand years and that there were perhaps several impacts, all unrelated to the extinction. Yet, it has been shown repeatedly that the impact and the extinction were synchronous (Schulte et al. 2010; Renne et al. 2013).

Those researchers who favor a single cause for the mass extinction at the K–Pg boundary emphasize the almost apocalyptic effects a bolide impact would have (Alvarez et al. 1995). This impact ejected considerable volumes of molten rock particles and dust into the atmosphere. Furthermore, it produced huge tsunami-type waves that devastated the coastal plains, and an immense fireball ignited vast wildfires. The dust particles would remain in the atmosphere for months, perhaps even years, leading to global cooling and darkening. Photosynthesis came almost to a halt, at least in plants adapted to higher light intensities. The fern spike recorded from many terrestrial boundary sections testifies to this sudden decline in higher plants and the spread of the ferns which could cope with darker conditions. As a consequence of the collapse of the ecosystems, first the consumers and then the carnivores died out within years. Those animals that did survive were preferentially small, unspecialized, opportunistic species that could feed on a variety of diets. That ecosystems were also severely and almost instantaneously hit in the marine realm is indicated by the patterns of the stable carbon isotopes across the boundary. These were previously interpreted as indicating an almost lifeless ocean after the K–Pg boundary ("Strangelove Ocean"; Hsu and McKenzie 1985; Zachos et al. 1989). Yet, marine productivity probably collapsed for only a few years (Alegret et al. 2012).

The normal succession in Caribbean coastal sections agrees well with the impact scenario (after Alvarez et al. 1995): above the Maastrichtian limestone, larger airborne particles (microtektites, glass spherules) were deposited first, then come tsunami deposits containing reworked Maastrichtian limestone and charcoal (from wildfires), and then dust-borne iridium and shocked quartz, and finally we see a return to normal sedimentation. Yet, a modified multiple-causes scenario seems at present to explain best the observed patterns (Archibald 2011; MacLeod 2013). Such a scenario emphasizes sea-level fluctuations, climate change, and continental flood-basalt volcanism, but accepts the Chicxulub as a devastating event that played a crucial role in the mass extinction.

Eocene–Oligocene Transition

In a diagram of Phanerozoic extinction intensities, the Eocene–Oligocene transition period barely stands out as an important event, and yet this time marked the most significant episode since the extinction of the dinosaurs (Prothero 1994). The Eocene was a time of warm temperatures, with widespread tropical forests, archaic mammals, and reptiles occurring above the Arctic Circle (Prothero 1994, 2006; Ivany et al. 2003). Within a time period of 10 Myr, this "greenhouse" world shifted to "icehouse," with decreased global average temperatures and markedly increasing seasonality, accompanied by major shifts in the biota of terrestrial environments and the seas (Berggren and Prothero 1992; Pälike et al. 2006; Zachos et al. 2008; Vandenberghe et al. 2012).

The record in the marine environment is one of a rather gradual turnover. A displacement of warm-adapted taxa by invading high-latitude forms is observable in both planktonic and benthic taxa and was obviously accelerated around the Middle–Late Eocene (Bartonian–Priabonian) boundary and within the Early Oligocene (Rupelian) (Berggren and Prothero 1992; Prothero 2006). As much as 90 % of the genera disappeared in some groups (Hallam and Wignall 1997). Fishes survived this period almost unaffected, while among the whales the more basal archaeocete whales were replaced by the first modern toothed and baleen whales (Prothero 1994).

On land, the flora changed between the Middle Eocene and Early Oligocene from widespread forests to open shrublands (perhaps with early grasses), and the leaf record as well as the amphibian and reptile fauna show a marked cooling and drying trend (Prothero 1994, 2006). Among the mammals, a fundamental difference between the Eocene and Oligocene faunas, the "Grande Coupure," has long been recognized (Stehlin 1909; Legendre and Hartenberger 1992). In Europe, there is a gradual replacement of archaic by modern mammals throughout the Late Eocene and Early Oligocene, with a pronounced peak of extinctions at the Grande Coupure (Hooker et al. 2004). This latter event is now dated to the Early (but not earliest) Oligocene (Prothero 2006). Almost all new taxa are immigrants from Asia, which could reach Europe after the closure of the Turgai strait in the Ural region. Similar trends are observable on the other continents (Prothero 1994, 2006).

High-resolution oxygen isotope studies over the past decades have considerably helped to clarify the climatic evolution from the Early Eocene to the Early Oligocene. Global temperatures reached a peak between 52 and 50 Myr ago, during the so-called Early Eocene Climatic Optimum (EECO). This was followed by a 17-Myr-long trend toward cooler conditions, with a dramatic increase in $\delta^{18}O$ at the Eocene–Oligocene boundary (Zachos et al. 2001; Vandenberghe et al. 2012). This latter shift in the oxygen isotope values reflects not only cooling but also a significant increase of the Antarctic ice cap. The first ephemeral ice sheets appeared already during the Late Eocene and were probably the result of both declining atmospheric CO_2 levels (DeConto and Pollard 2003) and an increasing thermal insulation of Antarctica. Plate tectonic movements had led to the separation of Australia and Antarctica and to the opening of the Drake Passage between Patagonia and Antarctica. By the end of the Eocene, the passage south of Tasmania was deep enough that the circum-Antarctic cold deep current could become established and the Antarctic ice cap rapidly grew (Prothero 1994, 2006; Ivany et al. 2003; Kennett and Exon 2004). Yet, on land, the extinctions associated with the Eocene–Oligocene transition were not simply the result of global cooling, increased seasonality, and increasing aridity but also a consequence of large-scale migrations. As an alternative or perhaps additional cause of the terminal Eocene turnover, impacts by comet showers have been proposed (Poag et al. 2003). Yet, the biotic turnover patterns do not correspond to an impact scenario (Ivany et al. 2003), and the Siberian Popigai (100 km) and the Chesapeake Bay crater (85 km) have now been dated as Late Eocene, when no extinctions occurred (Prothero 2006).

Pleistocene and Modern Extinctions

During the Pleistocene, between 2.6 and 0.01 Myr ago, the Earth witnessed large climatic fluctuations. Both plants and animals on all continents showed large shifts in their geographical distribution during this period, but the extinction levels were not above background values (Alroy 1999). This is true for such disparate taxonomic groups as insects, amphibians, reptiles, birds, and mammals. Yet, there is one major exception to this rule: the so-called mammalian megafauna (animals $>$ 44 kg).

Fifty thousand years ago, more than 150 genera of this megafauna populated the continents, but by 10,000 years ago, at least 97 of these genera were extinct (Barnosky et al. 2004; Koch and Barnosky 2006). There have been continued debates over whether these extinctions were caused mainly by environmental changes associated with climatic fluctuations or were the consequences of human impacts. It is undisputed that humans were responsible for the extinction of large mammals and large birds on islands such as Madagascar, Antillean, Mediterranean, East Asian Islands, and New Zealand (Barnosky et al. 2004; Burney and Flannery 2005). Here hunting and habitat fragmentation led to extinctions, even in the absence of climatic change.

An important aspect is that mammalian megafaunal species on all continents became extinct, but both magnitude and timing of the extinctions differed between continents (Roy 2001; Barnosky et al. 2004; Koch and Barnosky 2006). The extinctions were most severe in Australia where 14 out of 16 (88 %) giant marsupials succumbed. In addition, all seven genera of megafaunal reptiles and birds went completely extinct (Barnosky et al. 2004). Humans arrived on that continent somewhere between 71,500 and 44,200 years ago, and most megafaunal species became extinct before 40,000 years ago (Koch and Barnosky 2006; McGlone 2012). In North America, 33 genera (72 %) went extinct (Roy 2001) within a short time interval between 11,500 and 10,500 years ago, closely correlating with the arrival of Clovis-style hunters (Alroy 1999; Roy 2001; Koch and Barnosky 2006). In South America, 50 genera (83 %) vanished during the arrival and spread of humans about 12,900–10,000 years ago. In Eurasia (excluding Southern Asia), 9 genera out of 25 (36 %) became extinct during two pulses (45,000–20,000 years ago, 12,000–9,000 years ago). These extinction pulses correlate also with the spread and then the population increase of modern humans (Barnosky et al. 2004; Koch and Barnosky 2006). In Africa, the losses were relatively mild at only 8 genera (18 %). When considering only mammals $>$1,000 kg, the differences between continents are even more marked. In North America all four genera were lost, Eurasia saw the demise of four out of five, but in Africa, no such genus went extinct (Roy 2001; Koch and Barnosky 2006).

Many phases of human colonization were coeval with marked climate changes. Because earlier, similar climate changes were not accompanied by marked extinctions, hunting by humans (overkill) was proposed as the main mechanism responsible for the extinctions (Martin 1984), either by heavy and selective hunting ("Blitzkrieg") or through habitat fragmentation, nonselective hunting, and the introduction of exotic species ("Sitzkrieg"). The current consensus picture for megafaunal extinctions on the continents is that extinctions were most pronounced where a rapid spread and increase in *H. sapiens* populations coincided with marked climatic shifts (Burney and Flannery 2005). But it was not primarily large-sized but rather slow-breeding species (this is, in part, correlated with large body size), which were at the highest risk of extinction (Johnson 2002). Even if the proportion of deaths caused by humans was low at any one time, slow-breeding megafaunal mammals were driven to extinction.

Yet, the story is not over. Since the age of colonialization, the exploitation of nature has reached a new level, and the fate of the dodo (*Raphus cucullatus*) is just one very sad and telling example of human impact. This flightless bird was discovered in 1598 on Mauritius after Portuguese sailors first reached this island in 1507 and became extinct by 1690, not only by hunting but also by the introduction of domestic species, such as goats, pigs, and rats, which devoured the eggs and the young. The list goes on, and even extremely common species like the passenger pigeon in North America (*Ectopistes migratorius*) have proven to be no match for intensive hunting humans.

Starting during the epoch of industrialization, exploiting nature and destroying natural habitats have proceeded at an ever-increasing rate (Wilson 1994). The human impact on nature has become so profound and is already so visible in the stratigraphic record (Wolfe et al. 2013) that for the time since the beginning of the industrialization the new term "Anthropocene" was proposed (Crutzen and Stoermer 2000; Crutzen 2002). It became accepted rather quickly in the scientific literature (Steffen et al. 2011; Zalasiewicz et al. 2012; Ruddiman 2013). There is no question that current extinction rates for plants and animals have reached in the Late Anthropocene a level perhaps 2–3 magnitudes above background rates (Nott et al. 1995; Pimm et al. 1995; Ricketts et al. 2005; Barnosky et al. 2011). Scaling the available estimates of current extinctions up to a magnitude where we can compare them to past Phanerozoic mass extinctions reveals that if species losses continue at the present rate, 96 % of species will be extinct within just a few hundred or thousand years (May et al. 1995; Sepkoski 1997; "Sixth" extinction). This is the maximum estimate for species losses during the most severe of all the Phanerozoic mass extinctions, the one that occurred at the Permian–Triassic boundary! Yet, although the end-Permian mass extinction is no longer seen as a crisis spanning millions of years, current estimates are still on the order of a hundred thousand years. There is even further concern. As several episodes of mass extinctions have shown, even a moderate increase in global temperatures of a few degrees, if it happened fast enough, has proven fatal for life on the entire planet.

Conclusions

After more than 30 years of intensive research, the picture of life's diversification on Earth has attained an unprecedented level of accuracy. Much progress has been made in Precambrian research, notably in the study of the oldest fossils and their environment. Major input into studies of radiations and extinctions has come from geochronology, which has provided a new, accurate time scale. Other important developments have been the establishment of a new animal systematics and the considerable advances made in the dating of lineage splits.

The quintessence of diversity studies, the global diversity trajectories for the Phanerozoic, has been refined in many ways, and Sepkoski's classical, iconographic figure of the marine animals has recently come under scrutiny. Many of the dogmas are being reevaluated, a new database is being developed, and methodological problems are receiving considerable attention. What is needed for further refinement will especially be studies at the local level that take into account ecological data and ultimately can be assembled into a new global picture.

Mass extinctions have received a tremendous amount of attention since 1980, and for most of them, a consensus interpretation exists today. Emerging is that each extinction event had its own signature, and no common cause has been found. Hot topics at the moment are the diversification of the metazoans and the Cambrian and Ordovician radiations, and here we will most likely see much progress in the next few years.

Cross-References

▶ Fossil Record of the Primates from the Paleocene to the Oligocene
▶ Paleoecology: An Adequate Window on the Past?
▶ Quaternary Geology and Paleoenvironments
▶ Taphonomic and Diagenetic Processes
▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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Taphonomic and Diagenetic Processes

Gisela Grupe and Michaela Harbeck

Contents

Abstract

The recycling of matter within an ecosystem is a fundamental process and, therefore, fossilization of a body or its parts is always the exception to the rule.

G. Grupe (✉)
Department of Biology I, Anthropology, Ludwig-Maximilian-University München, Planegg-Martinsried, Germany
e-mail: g.grupe@lrz.uni-muenchen.de; asm.grupe@extern.lrz-muenchen.de

M. Harbeck
Bavarian State Collection of Anthropology and Palaeoanatomy, Munich, Germany
e-mail: m.harbeck@lrz.uni-muenchen.de

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The transition of organic remains from the biosphere to the lithosphere (=taphonomy) comprises the successive steps of necrology, biostratinomy, burial, and diagenesis. Focusing on the taphonomy of vertebrate skeletons, fossil types, and the main processes leading to preservation and/or destruction of a dead body and how these are intertwined are introduced. All in all, fossilization is not a random process. Almost all the first-order changes a dead body is subject to prior to fossilization may lead to alterations in size and shape of a skeletal part, which might be mistaken for artificial manipulations (pseudoartifacts). Taphonomic processes without doubt lead to a stepwise loss of information about the formerly living being. Today, methodological progress especially in the field of archaeometry permits the evaluation of a variety of lifetime parameters. However, deep insights into taphonomic, especially diagenetic, processes are the indispensable prerequisites.

Introduction

The recycling of matter is one of the fundamental processes of life. Fossils, on the other hand, are evidence for the possibility that either complete organisms or their parts may be transferred from the biosphere to the lithosphere with preservation of morphological and even biochemical features. With regard to the various biogeochemical cycles which are characteristic for ecosystems, fossilization is necessarily the exception to the rule.

Taphonomy

Taphonomy is the paleontological subdiscipline that unravels the processes an organism is subject to from its death until its recovery (Fig. 1). The term "taphonomy" was introduced by the Russian paleontologist Efremov (1940) as the study of the transition of organic remains from the biosphere to the lithosphere, whereby the etymological origin of the term from the Greek taphos = tomb implies the necessity that the dead body or its parts become buried sooner or later after death (note the origin of the term "fossil" from the Latin word fossilis = excavated, related to fadere = to dig, or effodere = to excavate). Carcasses that remain on the surface usually do not have a chance to turn into a fossil and will instead undergo complete decomposition. The preserved fossil record is greatly biased toward organisms which have durable, hard parts like mineralized tissues and to those organisms which occur in large numbers, hence with high population density. Fossilization is therefore not a random process. Taphonomy is a field of scientific research which is primarily dedicated to fossils, but today also relates to bioarchaeological remains. This is expressed by the flexible definition by Behrensmeyer et al. (2000), according to which a fossil is a "nonliving, biologically generated trace or material" that is studied "as part of the record of past life."

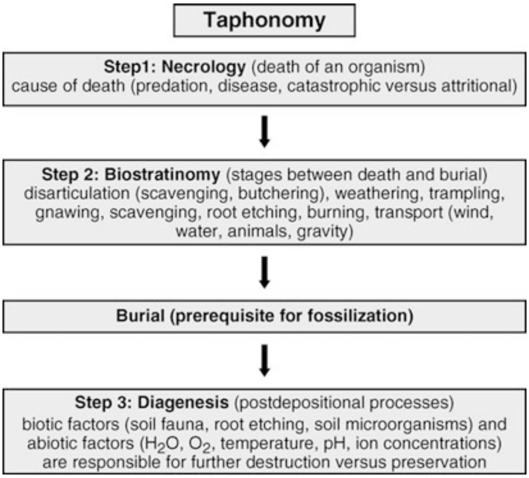

Fig. 1 The consecutive steps of taphonomy (cf. text)

Taphonomic Analysis

The first step of taphonomic analysis comprises *necrology*, the actual death of an organism. While most animals die *in toto*, entire plants frequently do not but rather shed parts like leaves or pollen, which may fossilize. After death, *biostratinomy* is responsible for the further condition of a carcass prior to its burial and includes processes like disarticulation (by scavengers or intended dismemberment by butchering), weathering and trampling, gnawing and scavenging, root etching, and even heat exposure (accidental or intended). Moreover, the body or its parts can be subject to transport by wind, water, animals, or simply to gravity, when it is exposed somewhere uphill. As a consequence, most fossils will be removed from their original context and the place of recovery will differ from the place of individual death. In the case of hominins, this situation changed not before humans started to intentionally bury the dead. Finally, the bodily remains become buried, and *diagenesis* sets in. Diagenetic processes involve all interactions of the dead body or its parts with the surrounding sediment, which either end up in the complete disintegration and dissolution of the body or in its lithification. “Diagenesis” is a term derived from the earth sciences and refers to the biological, chemical, and physical changes that take place in sediments after the deposition of the body and which may end up in lithification.

In this narrow sense, diagenesis also applies to fossils. Today, this term is frequently used in its broader sense, is synonymous with “decomposition,” and refers also to subfossil and prehistoric bones and to finds of forensic relevance. The state of preservation of a dead tissue will give clues to burial conditions, to burial practices, and sometimes even to *ante mortem* conditions such as cause of death or existing diseases. *Ante mortem* injury or infection or any pathology which causes tissue breakdown during life is likely to accelerate decomposition. Even after lithification, fossils may show up on the surface due to erosion, where they are again subject to weathering and trampling. Taken together, the taphonomic processes lead to a stepwise loss of information about the formerly living being or at least to a decline of the integrity of the information through the many ways that the evidence can be altered (Reitz and Wing 1999). However, the statement by Shipman (1981a, p 3) “in short, through death most evidence of the interesting information about animals what they look like, what they eat, how they move, where they live, and so on – is lost” now requires, more than 30 years later, some revision: Methodological progress, particularly in terms of archaeometry, permits the evaluation of several of the abovementioned parameters, including genetic relationships in cases of preserved DNA. But it becomes also clear that any research on the molecular or crystal level necessitates deeper insights into taphonomic, especially diagenetic, processes. Thus, the early statement by Weigelt (1927) that taphonomy and disintegration will give clues to the paleoenvironment in which the fossils were buried still holds today, and taphonomy has now become an integral area of paleoenvironmental research.

Nonetheless, taphonomy has largely changed from a paleontological subdiscipline into a scientific field of its own, where research mostly focuses on either biostratinomy or diagenesis. Since the 1980s several books covering this topic provide proof of the development of this field of research (Behrensmeyer and Hill 1980; Binford 1981; Brain 1981; Shipman 1981a; Allison and Briggs 1991; Donovan 1991; Lyman 1994; Martin 1999). Taphonomic analyses are also of great importance for archaeozoology, since animal bone deposits are usually the remainders of killing or butchering sites or village or home-based refuse. The animal bones are characterized by several kinds of manipulation before being deposited, and the individual animals have been transferred from the living community into the archaeological deposit (Reitz and Wing 1999). With regard to the aims and scopes of this handbook, this chapter concentrates on the taphonomic and diagenetic processes acting on the vertebrate skeleton, since the mineralized parts of a body have a higher probability of turning into a fossil than soft tissues. However, depending on the mode of preservation, the latter may also leave their traces.

Modes of Preservation

Several modes of preservation exist, which are briefly explained in the following sections.

Mineralization

This involves organic matter and necessitates exposure to water. Organic matter is gradually infiltrated and replaced by minerals derived from the watery environment, and mineralization results in the preservation of the shape of the organic component, sometimes down to individual cells (Nicholson 2001).

Carbonization

This results from heat and/or pressure, which removes all volatile organic components and leaves nothing but a carbon layer. This way, coal is generated from dead plant tissue.

Permineralization or Petrification

This is the result of the infiltration of natural hollow spaces of plant tissue, such as the xylem of woods, by infiltration and precipitation of exogenous minerals. If this exogenous material is made out of silica, wood will petrify.

Recrystallization

In its narrow sense, this is a process during which original mineral crystals change in size and shape, mediated by temperature and pressure. The chemical composition, however, is not changed, as in the case of the change of aragonite ($CaCO_3$, rhombic crystals) into its more stable form, calcite ($CaCO_3$, trigonal crystals). After death, mineralized tissues may be subjects of a spontaneous rearrangement of the crystalline matrix. Since the crystals change in both size and shape, morphological details will not be preserved, and even destruction may occur. Frequently, the term “recrystallization” is used in a quite broad sense and refers to almost all changes of the mineral portion of a skeleton, including heteroionic substitution (see below).

Heteroionic Substitution or Replacement

This is a mode of preservation in the course of which the mineralized components of a body are substituted molecule by molecule, or ion by ion, with exogenous material. This process takes a long time because the original mineral has to first dissolve before it can be replaced by exogenous precipitates, like silica, which are less soluble. Morphological details will be preserved, contrary to recrystallization; hence, substitution may lead to a “perfect” fossilized skeletal part.

Molds and Casts (Authigenic Preservation)

These are special fossil types wherein a body part gets trapped into sediments which harden, while the original bodily tissue (mostly bone or shell) dissolves. Thus, a void is produced within the sediment, and its negative relief can preserve the impression of the former body part left on the still soft sediment. Hardening sediment, producing a cast (with a positive relief), may again infiltrate this void.

It is also possible that sediment infiltrates a shell or a hollow space of a skeleton, e.g., the brain case, and hardens while the shell or bone dissolves. The resulting mold will also have a positive relief as in the case of the brain cast of the Taung child. Under special circumstances, bodies may be preserved unaltered, like insects trapped into amber.

Trace Fossils

This special category can be defined as modifications brought about by activities of living organisms on substrates and therein. Trace fossils include gnawing and butchering marks on bones (feeding traces, see later) but mainly concern visible tracks of a no longer visible body (or its parts), like fossil rodent burrows, sleeping pits of hibernating cave bears, or the so-called bear polish, a gloss on stones resulting from the polishing action of bears' fur in narrow cave passages (for review, see Gautier 1993). The most famous such fossil in the paleoanthropological record is the preservation of the australopithecine footprints from Laetoli. Such impressions will be preserved when they are buried quickly. Rapid burial is less uncommon than sometimes assumed, since not only volcanic ash eruptions but also storms, floods, or landslides may cause sedimentation within hours.

In this sense, fossilized feces called *coprolites* (from the Greek copros = dung and lithos = stone) can also be included into this highly variable group of trace fossils because coprolites are the result of the metabolic transformation of living organisms (edible plants and animals) into feces that later fossilized. Coprolites from many animal species including dinosaurs have been recovered, and they are mostly preserved by mineralization after rapid burial. However, very old coprolites are not easily identified in terms of their origin, and this holds especially for the fossilized feces of omnivores. Coprolites suggested to be of hominin origin were, e.g., removed from the *Australopithecus africanus* site at the Olduvai Gorge, from the *Homo erectus* site at Terra Amata, and from a *Homo neanderthalensis* site at Lazaret. In none of these cases could their hominid origin be confirmed by conventional coprolite identification methods (cf. Trevor-Deutsch and Bryant 1978).

Bog Bodies and Mummies

These are not fossils in the narrow sense since they are not lithified. The development of bogs set in after the last glaciation and was driven by substantial precipitation and water masses set free from the melting glaciers. In such regions where precipitation exceeds evaporation, peat bogs are generated which are characterized by an acidic pH between 3 and 5. When precipitation accumulates in natural depressions close to the groundwater, fens develop the pH of which can reach alkaline values. As a consequence, bodies buried in fens exhibit well-preserved mineralized and keratinized tissues, whereby bodies from peat bogs suffer from an advanced demineralization of the skeleton but have well-preserved soft tissues due to tanning. The spectacular bog bodies are therefore recovered from peat bogs, where the polysaccharide sphagnan of the *sphagnum* mosses not only inhibits microbial growth but also plays a key role in the tanning process through interactions with amino acids. Since peat bogs are free of molecular oxygen with the exception of the most superficial layers, activity of oxygen-dependent enzymes is reduced or even completely inhibited (Freeman et al. 2004).

Natural mummification is bound to burial conditions which either rehydrate a dead body rapidly or which inhibit microbial growth and action (such as lack of oxygen, cold, dry heat, high concentration of heavy metals or toxic elements). This way, initial putrefaction will be stopped, and soft tissues will be preserved. Such natural mummification leads to dry mummies (desert dry soils, soils with high nitrate concentrations), crypt mummies (at constant ventilation and air flow), ice mummies (cold at high latitudes or altitudes, preferably in combination with low humidity), or salt mummies (in salt deposits). Moist conditions accompanied by a relative lack in oxygen may lead to moist preservation with soft tissues preserved in a collapsed and advanced state of degradation. Even in archaeological skeletons, brain tissue may be recovered from an otherwise completely skeletonized body. Obviously, the inner brain case, protected by the skull bones, constitutes a favorable microenvironment. In addition, the myelin layer of the nerve cells may play a role. Such preserved brains, however, are mainly preserved in a state of advanced adipocere generation (Papageorgopoulou et al. 2010).

Preservation by lithification is thus not a common fate of a dead body and will occur only under special circumstances. As a result, not all places in the world have the same likelihood of bearing fossils somewhere under the surface. For instance, the acidic soil conditions of densely forested areas do not permit fossilization at all. Karstic caves, on the other hand, are characterized by low-temperature fluctuations and slightly alkaline conditions, which constitute a nearly ideal environment for fossilization. Normally, however, complete decomposition is the fate of a dead body, and the speed of the processes involved depends on the local burial environment. The tissues will suffer from stepwise destruction, and some destruction usually precedes preservation.

Alterations of Dead Bodies

Abiotic and biotic factors may both be responsible for the alterations of dead bodies in the course of necrology, biostratinomy, and diagenesis. These processes are also referred to as "first-order changes" because they are independent from archaeological activities and are opposed to "second-order changes" which are under control of the archaeologist, such as choice of site (where to excavate), excavation technique, etc. (Reitz and Wing 1999).

Preburial modification of body parts is brought about by scavenging, gnawing, digestion, butchering, weathering, trampling, transportation, and heat exposure.

Postburial modifications are the result of the burial environment, which is characterized by the availability of water and oxygen, temperature, pH, abundance of microorganisms, faunal and floral elements, and ion concentrations. Many taphonomic changes may resemble pathologies or even intended manipulations and give rise to killing or cannibalistic scenarios – another facet of taphonomic research which is responsible for distinguishing a biological signal from a taphonomic alteration.

The amount of paleobiological information that can be deciphered from a fossil is a function of all three steps of its taphonomic history. For instance, the body of individuals that died of predation have a smaller chance of preservation because the mineralized body parts will undergo at least same partial destruction by chewing and stomach acid etching. In ideal, rare cases, individuals are caught in natural traps like the famous La Brea tar pits in California. Such sites can contain fairly large amounts of accumulated fossil bones (Shipman 1981a).

Catastrophic death due to flash floods, volcanic eruption, etc. has to be distinguished from attritional death by natural causes, since the age structure of the resulting bone assemblage will differ drastically. While catastrophic death leaves a sort of snapshot of a formerly existing animal community, attritional death will lead to an overrepresentation of the more vulnerable very old, very young, and diseased individuals (see chapter "▶ The Paleodemography of Extinct Hominin Populations," Vol. 1).

The majority of alterations to vertebrate skeletons later recovered in fossilized form are due to biostratinomical processes. The recovery of a nearly complete fossilized skeleton or even of several parts of the same skeleton (e.g., the case of *Australopithecus afarensis* AL 288-1 "Lucy," the "Nariokotome Boy," *Homo erectus* KNM-WT 15000, or *Ardipithecus ramidus* ARA-VP-6/500, "Ardi") is exceptional. Usually, single skeletal elements or their parts are recovered out of their former anatomical context, with the teeth constituting the majority of fossil finds. This is the result of the natural disarticulation sequence of a vertebrate body, which is altered and enhanced by predators or scavengers and which depends on the structure and composition of an individual bone. The teeth are more frequently found in fossil assemblages because they are small and buried rapidly, and the enamel is densely mineralized and therefore not prone to microbiological decomposition. The over- or underrepresentation of specific skeletal elements at the australopithecine site of the Makapansgat limeworks has already been stated by Dart (1957) and was confirmed at the Sterkfontein, Swartkrans, and Kromdraai sites, giving early rise to both experimental and fieldwork (Brain 1967). Still, a major concern of taphonomic studies is the differentiation between natural and cultural origins of bone accumulations. Experimentation, the results of which are necessarily interpreted by uniformitarian assumptions, is usually straightforward despite its inherent limitations (for review, cf. Nicholson 2001; Denys 2002).

The mobility of joints and the presence of more resistant tissues like tendons control the natural disarticulation sequence. First, the skull and limb bones are disconnected, followed by the ribs. Next, the limb bones and the lower jaw become disarticulated, and only when the final stage is reached, when weathering will mostly have already set in, does the vertebral column become scattered (Toots 1965).

Once skeletonized and disconnected, the resistance of individual bones toward further destruction is a function of bone density (Lyman 1984). At this stage, the process of destruction appears to be rather constant and less a function of the exact taphonomic context. Best preserved are skulls, followed by the shafts of limb bones and their denser epiphyseal parts, while the sternum, clavicle, and scapula are usually the least well preserved.

Preburial Modification Processes of Body Parts

Weathering and Trampling

When talking about weathering, most people intuitively think of bone exposed to climatic conditions while it is still on the surface and not yet buried. Sufficient evidence exists that disarticulation and fragmentation of skeletons are mainly of biogenic origin (Behrensmeyer et al. 2000).

In her pioneering fieldwork, Behrensmeyer (1978) defined six stages of bone weathering, from stage 0 (no cracking or flaking) to 6 (bones mechanically fall apart into pieces), but made it clear that weathering may destroy a bone *in situ* “either on surface or within the soil.” While it is a common occurrence that bones buried within the soil may still “weather,” although at a much slower rate, the main interest of paleontologists, anthropologists, and forensic scientists is to define the time a skeletal element has spent on the surface or how much time has elapsed until a bone assemblage was formed.

In their critical evaluation of Behrensmeyer’s weathering stages and the conclusions drawn from them, Lyman and Fox (1997) confirm the main factors governing bone weathering (size and density, species-specific texture, stability of the environment – three factors only, but enough to render the process quite complex) but clearly point out that one is still “a long way from safely inferring time of bone assemblage formation, let alone hominid behavior, on the basis of bone weathering data.”

In the course of the weathering sequence a bone undergoes while still on the surface, longitudinal fractures appear first, followed by fractures running transversely to the shaft of a long bone. Fragments which become abraded may resemble bone artifacts like needles and awls. Needlelike bone splinters even with holes, strongly resembling needles at first glance, may be the product of stomach acid etching after bone ingestion by scavengers (Sutcliffe 1970).

Experimental work revealed that trampling of a bone can produce scratches by sediment grains that strongly resemble cut marks. Real cut marks, in contrast, may be completely erased by trampling. This is another example of pseudoartifacts which have been mimicked by natural phenomena and which can lead to serious misinterpretations of a fossil. It has therefore been emphasized that a correct identification of cut marks is greatly supported by their location on a bone (site of ligament or muscle attachments) and by their microscopic features (Behrensmeyer et al. 1986).

Transportation

Although whole bodies can be transported away from the original place of death by such agents as floods, the likelihood of transport is much higher for disarticulated body parts. These are taken away by predators and scavengers or are relocated by wind currents or gravity. However, "water is perhaps the most ubiquitous taphonomic agent transporting, modifying, and accumulating remains" (Haglund and Sorg 2002). The authors emphasize that many fossil hominin finds, such as the Nariokotome Boy or the australopithecine "First Family," have been recovered from sand or gravel sediments deposited by moving water, which are highly suitable for rapid embedding and burial. Since water environments differ in current, temperature, depth, salinity, and other features, disarticulation sequences and decomposition processes of a dead body are difficult to predict. Experimental taphonomic work with human bones in an artificial flume, which constitutes an ideal and not a natural water transportation simulation, has revealed different transport groups of bones according to their size and shape (Boaz and Behrensmeyer 1976). This does not only lead to a removal of skeletal parts from their original place but also to a sorting of the bones in terms of their morphological properties. Certainly, water transport causes additional damage to bones, especially by abrasion in sediment-rich water.

Scavenging and Gnawing

It is the scavenger's business to clear dead bodies from a site. Spontaneously, one would think of middle-sized mammals, like hyenas, but also small rodents, toads, and some land snails are efficient scavengers. Many more species gnaw bones, mostly to meet their calcium and phosphorus demands. These include nonhuman primates, canines, weasels, raccoons, hyenas, cats, artiodactyls, squirrels, beavers, mice, rats, porcupines, rabbits, hares, varanids, and same desert tortoises (cf. Reitz and Wing 1999). Osteophagia is especially common in artiodactyls (cattle, red deer, reindeer, muntjac, camels, and giraffes) as a symptom of phosphorus deficiency in regions with low phosphorus content of parent rocks. Since the bones are chewed with the molars, such gnawed bones reveal a pattern resembling forks and prongs, which may again be mistaken for human artifacts (Sutcliffe 1973). Rodents, which have to wear their ever-growing incisors, leave very characteristic gnaw marks, preferably on the edges of the bone, in the form of parallel grooves. Bite marks left by carnivores do not occur as parallel grooves but as irregular grooves and pits (Fig. 2). Four types of tooth marks, namely, punctures, pits, scoring, and furrows, have been identified by Binford (1981). The trabecular parts of the bones may be completely consumed, and the thicker compact shaft will exhibit splinters and sharp, pointed ends. According to Shipman (1981a), carnivore tooth marks have a V- to U-shaped cross section. Bones that have been digested are eroded and pitted by stomach acids. They are usually of very small size and will mostly be recovered only by sieving feces or regurgitants.

Fossil bone assemblages raise the question whether the bones have been accumulated by scavengers or by hunters (natural vs. cultural accumulations), especially

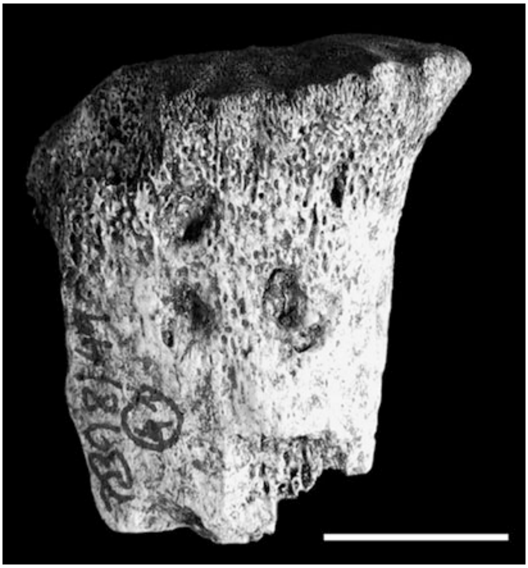

Fig. 2 Bite marks on the epiphyseal end of a tibia from a sheep/goat. Punctures are produced by canine teeth. Bones from juvenile animals like this one are rather soft and easy to chew. Note the additional cut mark at the *right lower end* of this fragment. The bone thus shows features of both butchering and gnawing (Photo: S. Bischler)

in the case of early hominins which are assumed to have practiced a mixed hunting-scavenging subsistence strategy (Shipman 1986). Extensive fieldwork revealed a fairly general consumption sequence of medium- to large-sized carcasses (Blumenschine 1986): Consumers proceed in two cycles from the back to the front of the carcass, consuming first the easily accessible, high-yield nutrients of the flesh and viscera and second the more difficult-to-access bone marrow and brain (Fig. 3). Blumenschine (1986), therefore, postulated a relationship between body part representation and an inverse consumption sequence. Bone assemblages due to hunting consist of more or less complete sets of body parts including those with large, easily accessible, meaty portions, whereas bone accumulations as a result of scavenging should consist of the less valuable parts of a carcass. A reevaluation of the hominin fossils recovered from Sterkfontein Member 4 (Pickering et al. 2004) in fact revealed that the paucity of postcranial remains, and the carnivore tooth marks on the fossils, strongly supports the “carnivore-collecting hypothesis” as the underlying mechanism for the accumulation of fossils at this site (cf. Brain 1981). Forensic studies also confirmed that canid disarticulation of human bodies follows this rather consistent sequence but may cover highly variable time spans. Total disarticulation was achieved between 5 and 52 months, and characteristically, the cranium could always be recovered in contrast to other skeletal elements (Haglund 1997).

Butchering

Butchering marks are cut marks produced by the tools utilized in the process of dismembering or skinning a carcass (Figs. 4a, b). While their cross section may be very similar to carnivore bite marks, they frequently exhibit fine, parallel striations

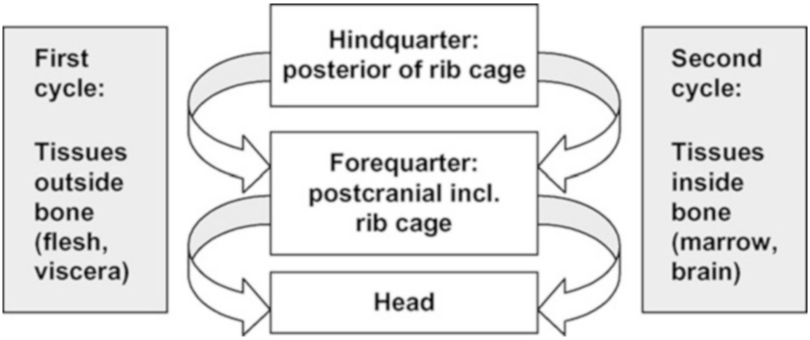

Fig. 3 General consumption sequence of carcasses according to Blumenschine (1986). Deviations from this general pattern are due to carcass size, age of the dead individual, and consumer type

Fig. 4 (**a**) Cut mark on a pig calcaneus (Photo: S. Bischler). (**b**) Damage to a pig tibia due to butchering that permitted access to the bone marrow (Photo: S. Bischler)

(Shipman 1981a, b) and have specific locations on the skeleton. According to Noe-Nygaard (1989), butchering marks reflect the tool type; hence, cut marks can be distinguished from scrape marks, hack marks, saw marks, and blows. Blows, especially, will fracture the bone and serve getting access to the bone marrow.

According to experiments carried out by Walker and Long (1977), cross sections through a cut mark permit the identification of the tool, and the shape and depth of cut marks vary with the applied force.

Other experiments by Bromage and Boyde (1984) open up the possibility of telling the directionality of cut marks on the bone, which would give clues to the handedness of their producers. However, the microstructural properties of the marks are highly dependent on the bone properties (type of bone, bone density, etc.).

Heat Exposure

Excluding natural fires, cremation as a special burial custom, and all cannibalistic scenarios, food processing is the most probable event when a bone is exposed to elevated temperatures for a prolonged time, and this will hold for animal bones in the majority of cases after hominins became capable of controlling fire. As long as a bone has been in direct contact with the heat source, burning and incineration will leave characteristic traces. Even after very short exposure, when charring is still absent, the denatured collagen will produce both longitudinal cracks (similar to those produced by weathering) and also transverse cracks in the bone, which are the result of recoiling of broken collagen fibers that had been previously under tension (Shipman 1981b).

Cremation has been practiced for millennia as a means of disposal of dead bodies (e.g., Bowler et al. 2003; Potter et al. 2011), and fire-exposed bone can also constitute a significant component of zooarchaeological assemblages. Thermally induced bone changes can be used to identify the circumstances and the temperature at which a bone was burned (Lyman 1994). The underlying temperature-induced changes in bone exposed to fire have been extensively studied and reviewed in numerous publications (e.g., Schmidt and Symes 2008; Ubelaker 2009); therefore, only the main changes induced by heat exposure of intact bone will be summarized here (as observed by Harbeck et al. 2011).

Between 100 °C and 300 °C, the bone dehydrates and an initial degradation of the organic matrix is observable. From 300 °C to 600 °C, the combustion of organic material and the loss of carbon in the form of CO_2 take place. As soon as the major proportion of organic material is gone (normally between 500 °C and 600 °C), structural rearrangements of the remaining chemical constituents in the hydroxyapatite structure of the cremated bone set in, and an increase in crystallite size can be observed. Between 600 °C and 800 °C, a sintering process takes place, which is sometimes accompanied by transformation of bone mineral to tricalcium phosphate.

These processes lead to the following macroscopic and histological changes, which permit the identification of a direct contact with a heat source for a particular bone: Bone changes its original color at temperatures ranging between 300 °C and 600 °C in the order of brown to black to gray, resulting from the oxidation of organic carbon. Above 800 °C, the bone shrinks, becomes "calcined," and develops a chalky constituency and white color (more detailed in Walker et al. 2008). Initial alteration of bone microstructure first becomes visible at 200 °C, manifesting itself in the form of small fissures. Above 300 °C, the lamellar structure is accentuated with a brown-black coloration, which vanishes around 500 °C. Microfissures are increasing in number, and at 800 °C and beyond, the original histological appearance entirely disappears (e.g., Hanson and Cain 2007). It should be noted that the quoted temperatures may vary according to the conditions and duration of the heat exposure (e.g., Walker et al. 2008).

The most probable event during which a bone is exposed to elevated temperatures for a prolonged time is food processing. During baking, roasting, or boiling, a bone is normally protected by surrounding flesh and not directly exposed to the fire. Hence, it will not even reach the initial stage of the thermal alteration outlined above. Boiled bones show no observable macro- or micromorphological changes (Munro et al. 2007; Roberts et al. 2002). Heating experiments in which bones were boiled for several hours revealed that protein loss is accompanied by increased crystallinity (Munro et al. 2007, 2008) and porosity (Roberts et al. 2002) – effects that are also caused by diagenetic deterioration.

However, even these changes require boiling times for extensive periods. Conventional boiling times have little or no physicochemical effects (Roberts et al. 2002). Therefore, unlike burnt bone, boiling, roasting, or baking leaves no *obvious* traces. Koon et al. (2010) suggest an inspection by transmission electron microscopy to detect collagen fibril changes caused by low temperatures to distinguish cooked and uncooked bones. Heating experiments with subsequent study of the changes induced by temperatures typical for food processing to date led to opposing results. Boiling whole bovine for several hours revealed that protein loss was accompanied by increased crystallinity and porosity, effects that might cause accelerated diagenetic deterioration (Roberts et al. 2002). Boiling fresh bones by Bosch et al. (2011) in contrast showed that structural changes of collagen should be responsible for the macroscopically evident smoothed surface of boiled bones and that porosities are rather closed, rendering the bone inaccessible to other decomposition factors, thereby reducing diagenesis. Whether the one or the other hypothesis holds true, another bias in terms of the composition of bone assemblages will have to be expected. However, diagenetic processes (see in the following section) may have precisely the same effects.

Postburial Modification Processes of Body Parts

Diagenesis

Diagenetic processes are controlled by the various features of the burial environment, that is, the availability of oxygen and water; temperature and its fluctuations; soil pH; the presence of soil flora, soil fauna, and especially soil microorganisms; and the availability of free ions (Fig. 5). Biodegradation can usually be differentiated from chemical degradation, but both pathways may be intertwined.

Biodegradation

Even after rapid burial, the general decomposition sequence of a dead body is maintained. Microorganisms present in the intestines, and bodily enzymes that

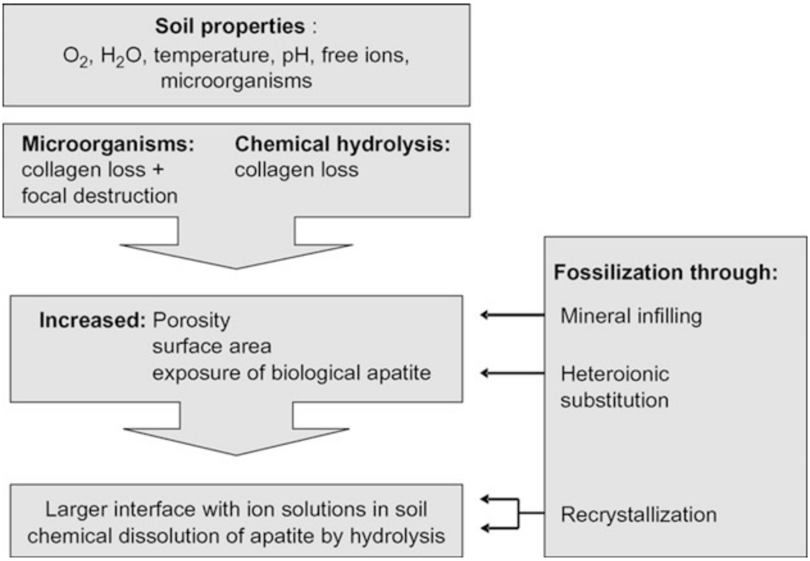

Fig. 5 Main parameters of diagenetic processes and possibilities for fossilization

continue working until the energy storage is exhausted, cause autolysis of the body's soft tissues. Autolysis also initiates putrefaction, a process mainly driven by bacteria. The next steps are liquefaction, disintegration, and finally skeletonization of the body (Dent et al. 2004). Moisture, temperature, and pH are responsible for the abundance of soil microorganisms, which get easy access to a bone by invasion through the natural hollow spaces. Microorganisms consume organic matter to meet their energy demands; therefore, the biological breakdown of a bone's organic constituents is also far from random (Balzer et al. 1997). Primary metabolic products of this organic matter metabolism are CO_2 and H_2O. In addition, many microorganisms are capable of secreting acid metabolites, which will subsequently dissolve the biological apatite, leaving characteristic destructive foci (Fig. 6), which were classified by Hackett (1981) into four different types. The majority of observed destructive foci are so-called linear-longitudinal tunneling and budded tunneling, followed by lamellate tunneling, which seems to be associated with budded tunneling, and fungi-associated Wedl tunneling (Jans et al. 2004). However, the higher resolution of electron microscopy techniques shows that most of these tunnels appearing in light microscopy are actually comprised of numerous smaller pores, often surrounded by a hypermineralized border (e.g., Turner-Walker 2012).

Many bacteria, like those of the genus *Streptomyces*, are capable of selectively cleaving collagen by their collagenases. Consequently, collagen is lost from the bone, leaving a higher porosity of the specimen. Together with the focal destruction, the surface area of the specimen is enlarged (Grupe 2001). Even in the absence of microorganisms, soil pH may lead to a slow loss of collagen from a bone by

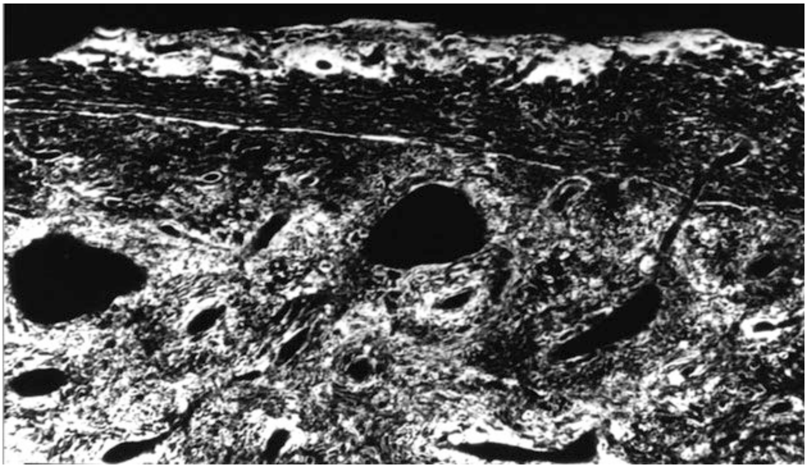

Fig. 6 Microradiograph of medieval human compact bone (Espenfeld, Thuringia), showing intensive focal destruction after microbial invasion

chemical hydrolysis (Fig. 7). Mineral infilling of the diagenetic porosities is considered a key mechanism leading to bone fossilization (Collins et al. 2002).

In general, it is plausible that microbial invasion of a buried bone plays a key role in bone decomposition, since prolonged microbial attack will prevent fossilization and accelerate breakdown. Since microbial activity is temperature and moisture dependent, warm and wet climates are less suitable for bone preservation. Exposure to excess humidity on the other hand will reduce the necessary oxygen supply, and microbial activity is suppressed. Microbiological diagenesis is also reduced in cold climates (Grupe 2001).

Mineral Changes

Normally, bone mineral is protected by its intimate association with collagen. Losing this association, it is vulnerable to dissolution and loss.

The enlarged surface area is an important factor in decomposition rates, since the exchange of matter (minerals and ions) between bone and the surrounding soil is facilitated. Exposed bone mineral may be subject to heteroionic substitution, supporting fossilization. Several elements are prone to be taken up by the bone, especially F, U, and rare earth elements (REE), whereby the latter serve as indicators for considerable diagenesis (Metzger et al. 2004) (see chapter "▶ Paleosols," Vol. 1). More frequent, however, is the chemical dissolution of the apatite by hydrolysis, depending on the soil pH. This will result in free ions, mainly calcium and phosphate ions, which will either be leached from the bone by soil moisture and precipitation or be recrystallized as soon as a critical ion density is reached. This recrystallization and/or the preferential loss of smaller crystallites in the course of mineral dissolution leads to an increase of the bone's crystallinity, a most fundamental aspect of bone diagenesis. Newly formed crystals are generally more soluble

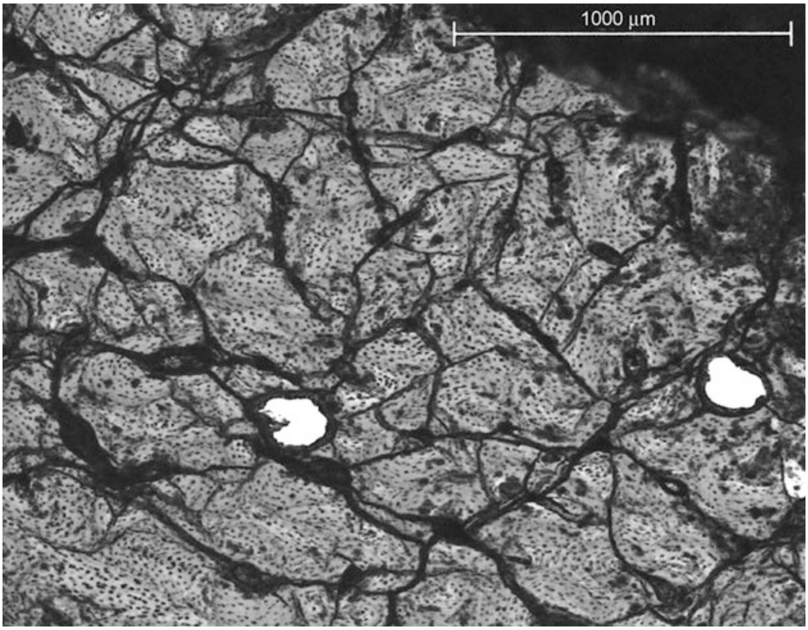

Fig. 7 Subfossil human bone (Göbekli Tepe, Anatolia, 9,500–8,500 cal BC). While the microstructure is well preserved with the exception of several microfissures, this specimen did not show any birefringence under polarized light. No collagen was retrievable from this specimen (Photo: S. Dummler)

than the original bone mineral, and disintegration proceeds. This holds, for instance, for the transformation of the original bone mineral, a calcium-deficient hydroxyapatite [$Ca_5(PO_4)_3(OH)$] into brushite [$CaHPO_4 \cdot 2H_2O$] as described by Herrmann and Newesely (1982). However, recrystallization may also lead to more stable mineral configurations and is therefore a means of fossilization: As soon as bone mineral is no longer subject of *in vivo* conditions, its crystallites recrystallize spontaneously into larger crystals (Berna et al. 2004), thereby decreasing its solubility. They nevertheless maintain a rather large surface which exhibits a considerable cation exchange capacity once exposed. As the organic components of bone (mainly collagen) are subsequently lost in the course of diagenesis, the thus generated intracrystalline porosity may be closed by the growing apatite crystals, which reduces the surface area available for ionic exchange. In a fully recrystallized bone, a minimum of 25 % of its volume must have been filled with exogenous, secondary minerals (Trueman et al. 2008). Together with other substitutions, such as F^- ions substituting type A carbonates at the OH^- position, such recrystallization may reduce the mineral solubility and enhance the chances for fossilization. According to Trueman et al. (2008), organic loss is the rate-limiting step, since the related exposure of crystals permits for the adsorption of exogenous ions with subsequent recrystallization. By an experimental study, Berna et al. (2004)

determined a quite narrow, alkaline pH range between 7.6 and 8.1 (the so-called recrystallization window), where the original bone crystals dissolve and recrystallize into another form of carbonated hydroxyapatite. As a consequence, and as a rule of the thumb, a bone will remain well preserved in sediments with a higher pH than 8.1, well preserved but with recrystallization in alkaline to neutral conditions, and will be totally replaced by authigenic apatite at pH values below 7.5. This, however, does no longer hold when recrystallization happens under inclusion of exogenous ions and formation of more stable phases (Berna et al. 2004). Diagenetic changes of the bone mineral phase are usually assessed by X-ray diffraction (measurement of the crystallinity index) or Fourier transform infrared spectrometry (measurement of the splitting factor).

In sum, the many parameters which characterize the burial conditions of vertebrate hard tissues and their change over time are responsible for the state of preservation at the time of excavation. In general, time elapsed after burial is a less crucial factor than the sediment conditions, whereby even small changes of some parameters such as pH may have considerable impacts.

Preservation of Biomolecules

In the course of the past few years, technological improvements led to a massive increase of ancient biomolecule research, especially in the field of DNA (e.g., Hofreiter et al. 2012).

It is, for instance, now possible to retrieve nearly complete genomes from more than 30,000-year-old Neanderthal bones (Green et al. 2010). This ancient DNA is highly diagenetically altered and persists only in low quantity in the form of highly fragmented molecules with chemically modified bases that may change the original sequence (see chapter "▶ Ancient DNA," Vol. 1).

For this reason and due to the high risk of contamination with modern DNA, the field of ancient DNA research has seen a lot of controversy as to which data sets can be considered as authentic and which not (e.g., review in Gilbert et al. 2005). Especially reports of DNA preservation in million-year-old fossils were mostly not confirmed (review in Willerslev and Cooper 2005).

There are several factors that influence DNA long-term survival. Besides the early postmortem enzymatic breakdown of DNA, the most common causes of damage are hydrolysis and oxidation. These processes depend on the presence of free water and oxygen, and their rate is increasing with increasing environmental temperature. Therefore, the best preserved DNA is usually found in cold environments. The oldest ancient DNA fragments recovered so far originate from 450,000- to 800,000-year-old Greenlandic ice cores (Willerslev et al. 2007). Because the burial conditions of these samples should have been close to being optimal, they represent the currently accepted limit of DNA survival. Allentoft et al. (2012) calculated a DNA decay rate using radiocarbon ages and measures of DNA integrity of moa bones. For room temperature, they estimated the half-life of DNA to be 521 years, while a short fragment of DNA (30 base pairs in the bone) will have a half-life of 158,000 years at −5 °C. This implies that DNA fragments in the bone may still be preserved in samples deposited in deeply frozen environments more than one million years ago. However, the study also shows that it is extremely unlikely to successfully sequence DNA fragments from millions of years old fossils, like dinosaur bones. Currently the oldest mammalian DNA sequenced so far comes from a jawbone of a polar bear buried in permafrost soil and dated around 120,000 years (Lindqvist et al. 2010).

There is also an ongoing discussion regarding the possibility of long-term survival of proteins in fossils, which reminds on the early days of ancient DNA research. In 2007, Asara et al. (2007) reported the detection of collagen peptides in a 68-million-year-old *Tyrannosaurus rex* bone by shotgun proteomics, and Schweitzer et al. (2009) have recovered protein sequences in an 80-million-year-old hadrosaur fossil. However, the discovery of intact protein in such an ancient sample has been called into question (e.g., Buckley et al. 2008; Pevzner et al. 2008).

In environments protected from microbial attack, chemical degradation plays the major role in collagen deterioration. Here, the primary process is the hydrolysis of peptide bonds which leads to the formation of protein fragments. But the rate of collagen degradation in the bone is slow because of its intimate association with the bone apatite. This association stabilizes the collagen fibrils, which is also evidenced when heated: Unmineralized collagen will melt at a temperature of about 68 °C, while mineralized collagen will not change until 150 °C is reached (Nielsen-Marsh and Hedges 2000). Therefore, in the absence of enzymatic degradation, collagen may persist in bones for many thousands of years particularly in cold environments. However, by all means collagen will undergo slow chemical hydrolysis which can be accelerated by increasing temperatures. Experimental diagenesis suggests a maximal collagen survival at 10 °C between two and seven million years (Buckley and Collins 2011). Long-term survival for longer time periods would require an as yet unknown alternate mechanism of preservation (Hofreiter et al. 2012).

When microbial activity and mineral dissolution are involved, the collagen molecule will degrade much faster. In this case the amino acid profile of collagen can be considerably altered, since microorganisms preferably tend to metabolize amino acids with a higher number of carbon atoms as a source of energy (Grupe 2001). This may also lead to shifts of carbon and nitrogen stable isotope values, which are commonly used for the reconstruction of dietary patterns of ancient populations (for a recent review see, e.g., Schwarcz and Schoeninger 2011). In order to assess potential diagenetic alterations or collagen contaminations, several criteria such as the molar C/N ratio are usually applied.

As the study of ancient biomolecules is both time-consuming and cost intensive, an expedient preselection of samples containing well-preserved target biomolecules would be useful as a screening tool in the situation when a large number of specimens are available and need to be assessed. Many studies, therefore, attempt to define easily obtainable predicators for molecular preservation like microstructural preservation or UV autofluorescence of the bone (e.g., Hoke et al. 2011). Numerous methods, such as collagen content measurement, crystallinity index analyses, and thermal age calculation (e.g., Götherström et al. 2002), have been suggested as marker for DNA survival. Particularly the extent of racemization of aspartic acid has widely been used for an assessment of DNA degradation (based on Poinar et al. 1996). Recently, the correlation between this measure and DNA preservation has been reassessed in some studies (Collins et al. 2009; Fernández et al. 2009), all concluding that the racemization of aspartic acid cannot be seen as an efficient marker for DNA preservation. Such disagreements are evident for nearly all proposed diagenesis marker showing that the underlying mechanism of degradation and the relationship between DNA, collagen, and hydroxyapatite are complex and need further clarification (see also Campos et al. 2012).

Conclusion

As time progresses, the conditions of a burial environment may change considerably. Therefore, any excavated bone specimen exhibits a certain status quo of its diagenetic history, which is hard to unravel in detail. Considering the gross diagenetic processes, it is obvious that certain environments are more suitable for preservation (anoxia, dryness, cold temperatures), while others enhance decomposition. It is a common experience that rather young archaeological bones may be much less well preserved than older ones. First, the simple explanation holds that a well-preserved or even fossil specimen must have been buried in a preserving environment. Second, diagenesis should also be considered a self-limiting process in many cases, especially when the burial environments are favorable for mineral infillings, recrystallization, and ionic replacement. The majority of recovered specimens will have undergone diagenesis to a certain degree.

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Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction

Julia Lee-Thorp and Matt Sponheimer

Contents

Abstract

In this chapter, we focus our attention on the potential links between hominin evolution and environmental change in Africa as revealed by stable light isotope evidence. We begin with an exploration of some of the gaps to which isotope approaches may be applied to good effect and follow with an overview of the principles and the materials typically available for analysis. The results for carbon isotope ratios of pedogenic carbonates and faunal enamel have now pushed back the emergence of C_4 grasses, and thus more open environments, to ca. 9 Ma. These data also show that in spite of a trend toward more open

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J. Lee-Thorp (✉)
Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, UK
e-mail: julia.lee-thorp@rlaha.ox.ac.uk

M. Sponheimer
Department of Anthropology, University of Colorado at Boulder, Boulder, CO, USA
e-mail: sponcu@gmail.com; matt.sponheimer@colorado.edu

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grassy environments observed from the Pleistocene and Pliocene records, consideration of the Late Miocene and Early Pliocene sequences as well suggests that proportions of grassy and forest habitats fluctuated on very broad timescales. New high-resolution biomarker records from Olduvai, and a single speleothem record from South Africa, show that, within the broader framework, shifts also occurred on shorter, orbitally controlled timescales. Faunal data indicate that herbivore families adapted to emerging C_4 resources at very different rates, with hominins showing signs of engaging with C_4 biomass only after 4 Ma. Aridity indicators reflect generally dry and warm conditions in East Africa, but the relationship between humidity and aridity on the one hand, and forest or open grassy cover on the other, varies for different environments. All lines of isotopic evidence from East and South Africa suggest a significant change to more open, grassy ecosystems ca. 1.8 Ma, broadly concordant with the emergence of *Homo ergaster*.

Introduction

It is widely accepted that understanding the environments that hominins inhabited provides essential contextual information to help us comprehend evolutionary trends. Most obviously, we need the environmental context to tell us about the kinds of opportunities available for the basics of life – food, water, and shelter – and the biological and the technological means to obtain these things. Next, we should consider how environmental and climate shifts have influenced the course of hominin evolution and that of other coeval fauna. Here, paleoenvironmental studies must take a broader, more long-term view. Large-scale, global climate shifts are often invoked as major influences acting on evolutionary pathways (e.g., deMenocal 2004, 2011), but in practice demonstrating the linkages is not straightforward (Feibel 1997). Firstly, climate is one of a number of forces acting on topographically complex landscapes and their floral and faunal communities. Further, climate and environmental evidence on land is patchy in time and space, so that what we observe are but short glimpses. This problem is exacerbated by the difficulties of establishing chronology with confidence.

One of the ways to address this problem is to take a much broader perspective that can discern patterns and hopefully process, from local noise. At the same time it's worth bearing in mind that behavioral (and biological) responses of hominins occur at the local level, which is the most important for understanding the lives of individuals. In other words, scale is important, both geographically and temporally. In this chapter we focus our attention on paleoenvironments of Africa, for the obvious reason that much of early hominin evolution occurred in this vast continent.

Standard investigative tools for reconstructing paleoenvironments at the site level rely strongly on geological context, faunal abundances, and, where possible, floral indicators such as fossil wood or pollen, as indicated elsewhere in this volume. All of these approaches naturally have their own advantages and constraints. For instance, although vertebrate faunal abundances provide essential indications about local faunal composition, the material is strongly filtered by the accumulating agents and by preservation. Additionally, interpretation of habitat preferences is hindered by poor knowledge of the ecology of extinct animals, for which there are often no modern analogues. In fact, we very often do not understand enough about the habitat requirements of modern congeners where they exist (see Cerling et al. 2003; Sponheimer et al. 2003). Here, stable isotope approaches can contribute complementary evidence that allows more precise identification of faunal dietary and hence habitat preferences.

There are greater challenges in placing these site- or regional-based occurrences into the context of climate and environmental evolution over the period of interest to students of human evolution, from the Upper Miocene onward. The evolution of global climate over this period and its pace and rhythms are largely understood from marine sediment cores. Ice-core records have revolutionized our understanding of the scale and rapidity of atmospheric and temperature shifts, but most reflect high-latitude conditions in the Late Pleistocene, with the exception of the 750 Ka EPICA core. How do spatially heterogeneous African environments reflect these global shifts reflected in marine sediments and ice cores, and how do we connect them?

Some marine sediment records near continental margins, fortunately, contain material derived from the adjacent continent, which provide direct, sequential information about continental conditions. The highly variable quantities of windblown Saharan dust in cores off Northwest Africa reflect a multiple alternating sequences of hyper-arid and humid conditions in the Sahara from the Miocene onward (deMenocal 2004, 2011). The most recent moist episode, the “African Humid Period” (AHP), is now constrained to between 11.8 and 4.9 Ka right across the Sahara and eastern Africa (McGee et al. 2013). The pace and intensity of shifts has been established from a series of well-dated, continuous marine records; the results point to strong orbital, particularly precessional, control over the intensification of monsoons that bring moisture to West, Central, and East Africa. Similarly, windblown pollen in marine cores off tropical West Africa provide the clearest view of the pattern of contraction and expansion of West African equatorial forests in the Pleistocene (e.g., DuPont 1999).

According to known site distributions, there are fewer well-dated continuous continental records in areas where hominins lived. Here the East African lake systems are exceptional, with sedimentary records for lake levels and lake conditions. The presence or absence of East African lakes is, however, influenced by tectonic activity in addition to rainfall shifts (e.g., Bergner et al. 2009; Trauth et al. 2009), leaving frequent long absences of any information. In spite of the discontinuities, opportunities exist. For instance, precise Ar/Ar dating of exposed diatomite beds has pointed to precessional control of extinct lakes in the Late Pliocene in Kenya (Kingston et al. 2007). The extensively studied sedimentary and lake system sequences associated with Olduvai Gorge ca. 1.8 Ma show strong environmental shifts on millennial scales (e.g., Ashley 2007). More universal information about the evolution of the terrestrial environments closely tied to hominin sites emerges from faunal abundance data (e.g., Vrba 1985, 1988; Behrensmeyer et al. 1997; Reed 1997; Bobe and Eck 2001). Vrba's "turnover-pulse" hypothesis postulating a direct link between evolutionary trends in bovids and climate shifts ca. 2.4–2.6 Ma (Vrba 1985) was based on bovid abundances, as were studies that challenged it (Behrensmeyer et al. 1997; Bobe and Eck 2001). In special circumstances pollen profiles are well preserved enough to provide detailed floral sequences (e.g., Bonnefille et al. 2004).

Stable light isotope-based methods can help to address some of the gaps. Biogeochemical tools have several advantages: they are versatile and can be used to study many different archives, and they produce qualitative and quantitative data. Stable light isotope applications to paleoenvironments in general have been extensively reviewed in the literature, and the field is broad (for a global review see Koch 1998). Our intention here is to restrict discussion to some key examples that we believe have made, or look set to make, substantive contributions to understanding the environmental context of hominin evolution. They reside principally in the area of shifts in floral composition, particularly in the relative abundance of C_4 grasses in the flora and implications for open or closed habitats and the important climate features of humidity or aridity. Since the last edition of this handbook series, significant advances have been made in documenting these features at different scales. We concentrate on examples reliant on materials from hominin or paleontological sites or from sequences that are closely associated in space and time.

Isotopic Environmental Indicators

This section provides a brief overview of the main isotopic environmental indicators and the sample materials that are used to provide indications of prevailing conditions. We limit discussion to the principles as they apply to each potential archive.

Basis of Stable Isotope Tools

The stable light isotopes of principle interest as environmental proxies are the isotopes of hydrogen, carbon, nitrogen, and oxygen. In all cases, the chemistry of the different isotopes of an element remains the same as chemical properties are controlled by electron configuration. But among the light isotopes, the mass difference owing to one or two extra neutrons is sufficient to cause small but predictable differences in the rates of physicochemical reactions, resulting in partitioning of isotopes. If the starting materials and the products of a reaction are partitioned, or facilitating enzymes are sensitive to mass, isotopic fractionation occurs.

Hydrogen **(D/H) and** ***Oxygen*** **($^{18}O/^{16}O$) Isotope Effects**

Fractionation of *hydrogen* (D/H) and *oxygen* ($^{18}O/^{16}O$) isotopes[1] in nature follows similar patterns because the isotope effects are dominated by the processes undergone by water – evaporation, condensation, and freezing. The magnitude of fractionation in precipitation is controlled largely by temperature for both isotopes, but isotope effects are greater for hydrogen because of the larger mass difference between deuterium (D or ^{2}H) and hydrogen (^{1}H), compared to oxygen (^{18}O and ^{16}O). Water vapor evaporates mostly from low to midlatitude ocean surfaces, and sea surface temperature of the oceanic source influences isotopic ratios of moisture-laden weather systems (Dansgaard 1964). The subsequent transport of the weather systems across the continent induces further (negative) fractionation related to the distance traveled, mountains crossed, and height and temperature of rain clouds (Dansgaard 1964; Rozanski et al. 1993). Evaporation has the opposite effect, leading to enrichment in the heavier isotopes. It is an important process in arid environments where water deficits are high. Soil- and groundwater isotope values reflect this history, as do those of carbonates precipitated from these waters, with the additional influence of temperature, since fractionation during carbonate precipitation is temperature dependent (Craig 1953). In plants, evapotranspiration leads to isotopic enrichment, which is enhanced under hot, dry, low relative humidity conditions, and is passed on to oxygen and hydrogen bound in plant sugars (Yakir 1992).

Carbon **($^{13}C/^{12}C$) Isotope Effects**

Carbon ($^{13}C/^{12}C$) isotope fractionation provides fundamental information about pathways in the terrestrial carbon cycle. Of most interest to African ecosystems is the isotopic distinction between plants following the C_3 and C_4 photosynthesis pathways. The RuBisCO (ribulose bisphosphate carboxylase oxygenase) enzyme involved in catalyzing the conversion of CO_2 to plant sugars discriminates strongly against $^{13}CO_2$. This results in low $\delta^{13}C$ values in plants using the ancient C_3 (or Calvin-Benson) pathway alone (Farquhar et al. 1989). Some families and genera have evolved a mechanism to first concentrate and fix CO_2 by means of another enzyme, PEPCase (phosphoenolpyruvate carboxylase), before it enters the RuBisCO cycle, so the isotope effect of this enzyme is weakly expressed (Sage 2004). As a result the $\delta^{13}C$ values of C_3 and C_4 plants are distinct (Smith and Epstein 1971). Almost all trees, shrubs and herbs, and temperate or shade-adapted grasses follow the C_3 pathway, while C_4 photosynthesis is common among grasses and sedge families in warm, often dry, environments with strong solar radiation in the growing season. C_4 plants exhibit a relatively narrow $\delta^{13}C$ range (from about -9 ‰ to -14 ‰, global mean of ca. -12 ‰), whereas C_3 plants are sensitive

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[1] Isotope ratios are by convention expressed in the δ notation, in parts per thousand (‰) relative to a standard: δX (‰) $= (R_{sample}\text{-}R_{ref})/R_{ref} \times 1000$, where $R =$ isotopic ratio. V-SMOW (Standard Mean Ocean Water) is used as the reference for D/H and $^{18}O/^{16}O$ in water, V-PDB (Peedee Belemnite) for $^{18}O/^{16}O$ and $^{13}C/^{12}C$ in carbonates and organic materials, and atmospheric N_2 (AIR) for $^{15}N/^{14}N$.

to environmental influences and show broader ranges (from about −22 ‰ to −38 ‰ at the extremes, with a global mean ca. −26 ‰) (Smith and Epstein 1971). A third photosynthetic pathway, crassulacean acid metabolism (CAM), fixes CO_2 by night and utilizes RuBisCO by day, so that $\delta^{13}C$ values can vary considerably. However, these plants are primarily succulents that are sparsely used by most mammals and are not considered important components of environments inhabited by hominins (Peters and Vogel 2005).

The carbon isotopes in plants are ultimately incorporated into the tissues of animals that consume them so that, for instance, grazers are isotopically enriched in ^{13}C compared to browsers, or frugivores. These distinctions are passed in turn to higher trophic level consumers. All tissues reflect the source of carbon but the diet to tissue offset (expressed as $\varepsilon_{d\text{-}t}$) differs among them (e.g., hair, liver, bone collagen, muscle).

Nitrogen ($^{15}N/^{14}N$) Isotope Effects

Nitrogen ($^{15}N/^{14}N$) isotope ratios reflect the pathways of the nitrogen cycle in soils, plants, and animals. Nitrogen enters the terrestrial food web via N_2-fixing bacteria in soils or plants, to form nitrates or ammonium ions that are utilized by plants. The net effect of the biological fixing of nitrogen into nitrates or ammonium ions utilized by plants, and subsequent loss from soils, is a slight enrichment in ^{15}N. The balance is strongly influenced and affected by local environmental conditions (Heaton 1987). A negative correlation between moisture availability and both leaf and soil $\delta^{15}N$ has been observed (Handley et al. 1999), but subsequent studies suggested instead that other factors such as plant taxonomy are more influential (Craine et al. 2009; Codron et al. 2013). Stepwise trophic enrichment about 2–6 ‰ occurs in animals.

Sample Materials

The sample materials most often analyzed for isotopes to infer environmental conditions consist largely of sediments or carbonates in close chronostratigraphic association with sites, and fossil bones and teeth within them.

Sediments

A history of overlying vegetation may be preserved for long periods in remnant organic compounds and pedogenic carbonates in paleosols (see Quade and Levin 2013 for a review). Carbon isotopes in the organic and inorganic components of soils systematically reflect differences between overlying vegetation following the C_3 and C_4 pathways, allowing calculation of the relative mix of woody and grassy plants on the landscape. $\delta^{13}C$ of paleosol organic matter, where preserved, is a reasonably direct reflection of the mean isotopic composition of the vegetation, with a slight enrichment in ^{13}C due to decomposition. Pedogenic carbonates form about 0.5–1 m below the active soil horizon from soil-respired CO_2 (Cerling and Quade 1993). The net enrichment (ε) in ^{13}C of 14–17 ‰ is made up of the combined effects of diffusion of plant-respired soil CO_2 (4.4–5 ‰) and equilibrium isotope effects associated with carbonate precipitation (9.5–12.5 ‰) (Cerling and Quade 1993). Pedogenic carbonate nodules are not formed in all soils; formation occurs in semiarid to arid conditions where mean annual rainfall is less than ~1,000 mm/a. Applying the diffusion model requires identification of "true" pedogenic nodules formed where diffusion enrichment is complete, that isotopic equilibrium can be confidently assumed, and that plant-derived CO_2 dominates rather than atmospheric CO_2 (Quade and Levin 2013).

While pedogenic carbonate isotope analyses have long dominated the sediment literature, leaf and algal wax biomarkers preserved in ancient marine and lacustrine sediments have emerged as an important new source for establishing plant composition and moisture regimes, based on carbon and hydrogen isotopes (Diefendorf et al. 2010; Feakins and Sessions 2010; Magill et al. 2013a, b). They have decided advantages – preservation in incremental sediments so that the sequence of shifts is preserved in situ – and fewer diagenetic effects than most other sources (Diefendorf et al. 2010). $\delta^{13}C$ values of the nC_{31} leaf-derived wax biomarker reflect dominant photosynthetic pathway of terrestrial plants, while heptacosane (nC_{17}) is derived from lake algae (Diefendorf et al. 2010; Magill et al. 2013a). Their hydrogen isotope ratios (δD) likewise express water sources and effects in soils, while algal values reflect more directly water balances within the lake system.

Cave Speleothems

Cave flowstones and stalagmites are composed of calcium carbonate formed from CO_2-rich seepage water degassing and precipitating in cave systems. Precipitation of carbonates is governed by temperature-sensitive equilibrium reactions, so speleothem $\delta^{13}C$ and $\delta^{18}O$ values reflect the proportions of C_3 and C_4 plants in overlying vegetation, isotopic composition of the water, and the temperature of cave carbonate formation, in a manner similar to pedogenic carbonates (Fairchild et al. 2006). Speleothems have advantages as they form in a protected environment, and they can be precisely dated using thorium-uranium or, more relevant for Pliocene and Pleistocene material, uranium-lead disequilibrium methods (Woodhead and Pickering 2012). Speleothems can yield near-continuous, high-resolution records of a quality unlike any of the other proxies discussed here, but their distribution is restricted to karstic landscapes and older records are unfortunately very rare.

Biominerals

Biominerals (bones, tooth enamel, and ostrich eggshell) preserve isotopic information about many of the processes and conditions to which an animal was subjected when it was alive, and they are abundant in most paleontological and archaeological sites.

Bones consist of an organic component made up mostly of a fibrous polypeptide, collagen (ca. 25 % by weight), while the embedded mineral makes up ca. 70 %. Collagen can be readily purified and analyzed for $\delta^{13}C$ and $\delta^{15}N$, but it decomposes rapidly (within millennia) in warm African environments. Bioapatites, the mineral phase, are weakly crystalline calcium phosphates with multiple substitutions that increase reactivity and solubility. The exception is fluoride, which has the opposite effect (LeGeros 1991). In vivo and *postmortem* substitutions affect the preservation of original isotopic composition in fossils. Enamel is far more stable than bone (Lee-Thorp and van der Merwe 1987), and consequently most isotope studies of fossils have relied on enamel as sample material. The component ions of interest are phosphate (PO_4^{3-}) and carbonate (CO_3^{2-}), with the latter occurring as a substitution in small amounts (3–6 %). Therefore, the isotopes available for study in this system are carbon and oxygen isotopes, the latter extracted from either PO_4^{3-} or CO_3^{2-}.

Biophosphate $\delta^{18}O$ was developed first as a paleotemperature tool, based on the rationale that body water $\delta^{18}O$ ($\delta^{18}O_{bw}$) reflects environmental or drinking water ($\delta^{18}O_w$), which can in turn be correlated with latitude and/or temperature effects on rainfall (Longinelli 1984; Luz and Kolodny 1985). In low- to midlatitudes, the effects of source, storm tracks, amount, and evaporation dominate as influences on precipitation and environmental water $\delta^{18}O$. Animals, however, also derive significant amounts of water and oxygen from their food (Kohn et al. 1996; Bocherens et al. 1996; Sponheimer and Lee-Thorp 2001), and we now know that thermophysiology, and drinking and feeding behavior, modulate the manner in which these environmental signals are reflected in bioapatites. For instance, obligate drinkers such as equids better reflect freshwater $\delta^{18}O_w$ values than do non-obligate drinkers such as giraffids that use a good deal of leafwater. The $\delta^{18}O_{phosphate}$ or $\delta^{18}O_{carb}$ of non-obligate drinkers is useful for exploring behavior in extinct forms. Additionally the isotopic difference between non-obligate and obligate drinkers, expressed as ES (evaporation sensitive) and EI (evaporation insensitive) versus local water deficit values, is exploited to develop an isotopic aridity (Levin et al. 2006).

Stable carbon isotope ($\delta^{13}C$) analysis of herbivore tooth enamel indicates the relative amounts of C_3 plants and C_4 grasses consumed. The framework for calculations of the proportions is based on our understanding of typical plant values today, the manner in which these are affected by climate variables, and the difference between diet and enamel values ($\varepsilon_{diet\text{-}en}$). There is some blurring here. Fractionation in C_3 (but not in C_4) plants is sensitive to climate conditions. C_3 plants are enriched in ^{13}C under hot, dry conditions and markedly depleted in ^{13}C in closed-canopy forests with low light intensity (Farquhar et al. 1989). Furthermore, $\varepsilon_{diet\text{-}en}$ is not *precisely* established and likely differs slightly for families; some observe +12 ‰ across many wild species (Lee-Thorp and van der Merwe 1987), while others have observed up to +14 ‰ in equids (Cerling and Harris 1999).

Still, this does not obscure the large $\delta^{13}C$ distinction between browsing and grazing forms and between occupation of open and forest-canopy habitats. Unlike pedogenic or cave carbonates, $\delta^{13}C$ values for fauna on their own do not represent the mix of plant types in a landscape, but rather what those particular taxa preferred. This is useful, for instance, in comparing the evolution of grazing across families, but in order to determine the proportions of plant functional groups in the environment (i.e., deduce the closed or open nature of prevailing vegetation), the data must be further reduced.

Ratite eggshell is a tough, mostly calcium carbonate structure which survives well for long periods (Ségalen et al. 2006). The carbon and oxygen isotopic composition follows similar "rules" to enamel, as it reflects carbon dietary sources in $\delta^{13}C$ and body water isotope composition in $\delta^{18}O$. Ostriches have an extremely low requirement for freshwater, while their eggshell reflects a narrow window of time reflected in the breeding season. Thus, ostrich/ratite eggshell $\delta^{18}O$ is a good aridity indicator, but the windows are narrow.

The following sections describe applications of isotopic approaches to paleoenvironmental issues of relevance in hominin evolution.

Emergence of C_4 Grasses

One important application of carbon isotopes has been to document the global expansion of C_4 grass systems from ca. 8 to 6 million years ago (Cerling et al. 1997). This ultimately revolutionized floral communities in tropical and subtropical regions across the globe, resulting in more open environments in many regions. The drivers of the shift are still unclear but global climate shifts must be implicated (Jacobs et al. 1999; Sage 2004). Given the profound nature of changes to African environments, and the timing of C_4 emergence and establishment prior to the probable age of the Last Common Ancestor (LCA), the importance of this floral shift to the hominin lineage has long been debated. The shift was first detected in pedogenic carbonate nodule isotope ratios from East Africa and Pakistan (Cerling et al. 1988; Cerling 1992; Quade et al. 1989), which showed a large-scale shift from C_3- to C_4-dominated systems around 7–8 Ma. Data from the Turkana Basin suggested the appearance of C_4 grasses about 7–8 Ma (Cerling et al. 1988), a pattern of first appearance apparently mirrored in $\delta^{13}C$ of fossil fauna in Africa, North and South America, and Pakistan (Cerling et al. 1997). Some authors have suggested an earlier first appearance prior to 12 Ma, based on carbonate nodules and fossil isotope values from the Tugen Hills (Kingston et al. 1994; Morgan et al. 1994), but these data are few and have not been replicated.

No older pedogenic carbonates have been found in the well-dated formations in the Samburu Hills and Lothagam in Kenya, but new enamel $\delta^{13}C$ data demonstrates that C_4 grasses emerged in this region at 9 Ma (Uno et al. 2011). The data prior to 9 Ma reflect only C_3 diets for all families, an observation consistent with $\delta^{13}C$ data for windblown terrestrial plant biomarkers in marine cores off NE Africa (Feakins et al. 2005). These data indicate only C_3 terrestrial plant waxes until 9.2 Ma, but a discontinuity immediately afterward prevents observation of a subsequent shift (Feakins et al. 2005).

One further notable observation from the Turkana fossil faunal data is that families clearly responded to the new resource at different rates (Fig. 1). While almost all families suggest responses at ca. 9 Ma, most are muted and variable, Equidae show a clear and immediate response, with $\delta^{13}C$ values rapidly reaching 0 ‰ by ca. 9 Ma (Uno et al. 2011). Gomphotheriidae, Rhinocerotidae, Hippopotamidae, and Bovidae show highly variable and less marked shifts, while

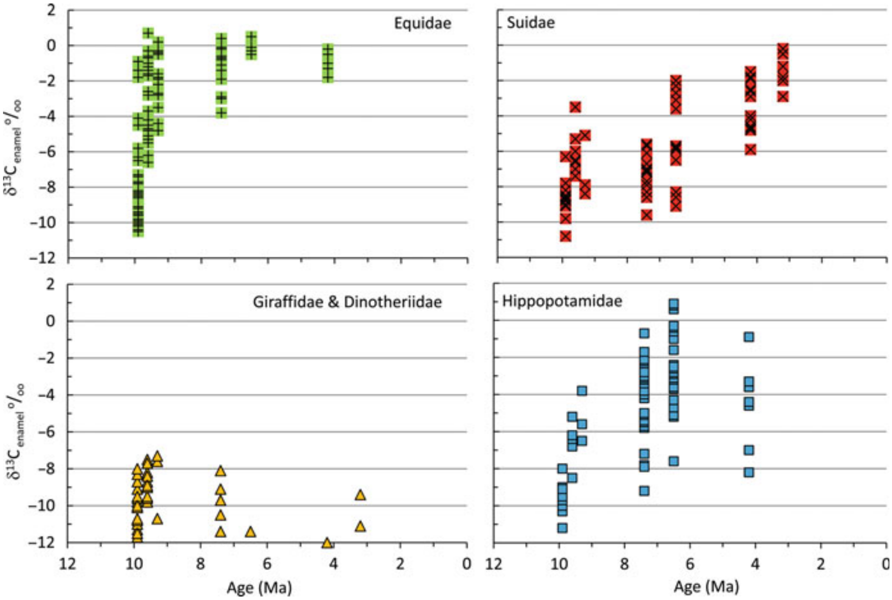

Fig. 1 The carbon isotope data for four families in the Lothagam/Samuru Hills/Nakali sequence, Kenya, are plotted against age in millions of years (Ma). The Equidae clearly show an immediate and rapid response to the new grass just prior to 9 Ma. Giraffidae and Deinotheriidae are plotted to show their relative invariance. Suidae and Hippopotamidae seemed to have responded slightly differently; in both cases earlier data are highly variable, but by 4 Ma and certainly before 3 Ma, the Suidae had adapted completely, while Hippopotamidae remain generalists. The data are from Uno et al. (2011). No attempt has been made to correct the $\delta^{13}C$ data according to palaeo-CO_2 values, as they did

Suidae show less enthusiasm for C_4 plants until much later – values shift modestly in the 6.5 Ma Upper Nawata Beds, and high $\delta^{13}C$ values emerge only in the Apak Beds (ca. 4.2 Ma). Deinotheriidae and Giraffidae remain dedicated C_3 feeders as also noted elsewhere (e.g., Cerling et al. 1997; Roche et al. 2013).

The age at which C_4 vegetation first appeared in southern Africa is unclear, as there are few Upper Miocene sites. Cerling et al. (1997) suggested an extension model in which first appearance of C_4 photosynthesis in low-latitude equatorial regions spreads subsequently to the midlatitudes. The present modest evidence seems consistent with this hypothesis. Ratite eggshell data document the emergence of C_4 and differentiation of the $\delta^{13}C$ records between the southern and northern Namib about 5–6 Ma, based on biostratigraphy (Ségalen et al. 2006). A large undated, collapsed cone speleothem in the Makapansgat Limeworks in South Africa indicates relatively invariant C_3 vegetation from the $\delta^{13}C$ record, suggesting that it was formed prior to C_4 grasses reaching this region at ~27°S (Hopley 2004). C_4 plants do not seem to have penetrated into the southwestern Cape of South Africa to any significant extent based on faunal $\delta^{13}C$ data from Langebaanweg at ca. 5 Ma (Franz-Odendaal et al. 2002). The much later hominin sites in the Makapansgat and Sterkfontein Valleys from ca. 2.8 to 1.2 Ma all show consistent but variable presence of C_4 grass from faunal $\delta^{13}C$ data (Lee-Thorp et al. 2007).

Overall, the main body of evidence is consistent with first expansion of C_4 grasses in lower latitudes at 9 Ma, expanding over the next few million years to midlatitudes (Cerling et al. 1997). The expansion of C_4 grasslands across large parts of the world demands a global explanation, but the nature of the drivers has remained curiously elusive. Cerling et al. (1997) and Ehleringer et al. (1997) proposed that plummeting CO_2 levels in the Late Miocene to levels below 500 ppm favored C_4 photosynthesis, based on the known tolerances of C_4 plants for lower levels of pCO_2. But evidence from marine cores suggests that pCO_2 levels were already lower (Pagani et al. 1999). It may be the case that reduction of pCO_2 in the late Middle Miocene/early Upper Miocene drove an earlier evolution of C_4 photosynthesis, but their later success may have been also assisted by climate factors such as solar insolation and enhanced rainfall seasonality.

Evolution of Open African Environments

A great deal of interest and controversy has surrounded the question of how forested versus open were the environments inhabited by early hominins, and the possible links to bipedalism and diet. The decline of large-scale dense forests and opening up of the African landscape is of course intertwined with the spread of C_4 grassy vegetation. Tree cover density has been shown to be strongly, linearly correlated with mean annual rainfall (MAP) in African savannas with a critical transition at 650 mm/a; below this, woody cover coexists with grasses and is sensitive to disturbance, while above it, savannas become "unstable" systems; MAP is sufficient for canopy closure and disturbance such as fire is required for coexistence with grassy vegetation (Sankaran et al. 2005).

Some years ago the "savanna hypothesis" held that forest shrinkage/savanna expansion in Africa was a primary driver of hominin bipedalism, because it was thought that these two trends occurred at about the same time. This hypothesis fell from favor once it became apparent that bipedalism emerged before 4 or 5 Ma, within, as it appeared, relatively wooded habitats (e.g., WoldeGabriel et al. 2001). Nevertheless there have undoubtedly been important and influential changes in the vegetation structures across Africa. The "turnover-pulse" hypothesis relied on the observed radiation of open-country, grazing bovids to draw inferences about shifts to more open landscapes in the Pliocene and Pleistocene (Vrba 1985, 1988). Vrba proposed that a shift to bovid lineages with open-country preferences between about 2.4 and 2.6 Ma coincided with the onset of Northern Hemisphere glaciation observed from marine oxygen isotopes in marine sediment core records (Shackleton et al. 1984). The idea of a turnover pulse has been challenged, however, although it is acknowledged that faunal changes occurred between 2 and 3 Ma (Behrensmeyer et al. 1997; Bobe et al. 2002). Moreover, we now know that the Bovidae radiation is one of several that occurred in response to the emergence of new C_4 grass resources and that these radiations occurred at different times.

A large body of work on pedogenic carbonates has shown that, after emergence in the Late Miocene, C_4 grasses persisted with high variability through the Pliocene (Cerling et al. 1988; Cerling 1992; Kingston et al. 1994; WoldeGabriel et al. 2000; Wynn 2000, 2004). They clearly became a more consistent component of the floral biomass at all sites after 2 Ma (Fig. 2a). A shift in $\delta^{18}O$ also occurs at about this time, suggesting that the source area and vapor transport pathway changed

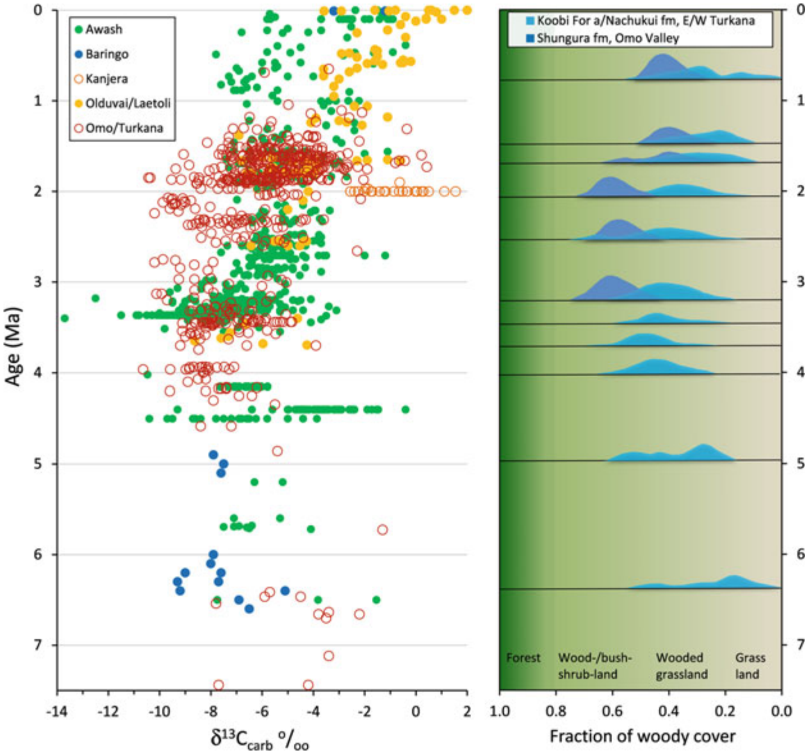

Fig. 2 Pedogenic carbonate nodule $\delta^{13}C$ data for locations in eastern Africa, where sufficiently large datasets exist, are shown plotted against chronology in the left panel. What is immediately apparent is the extreme variability, even at one time and place. Even so some regions were clearly more enriched in ^{13}C, suggesting unambiguously open landscapes (e.g., Kanjera), while others also fluctuate in time. For instance, the Awash data contains a positive excursion at about 4.2 Ma that cannot be due to internal variability. The panel on the right shows $\delta^{13}C$ data for Omo/Turkana region transformed to a normalized probability density function (PDF) in a series of time bins. The PDFs are plotted against "fraction of woody cover" on the horizontal and time (in Ma) on the vertical axis, based on a framework established from multiple modern locations as described in the text (Cerling et al. 2011). The Koobi Fora/Nachakui (*light blue*) and Shungura (*dark blue*) PDFs are shown separately as the latter preserves different environments compared to the rest of the Basin. This is apparent in the figure as Shungura Formation carbonates are consistently more depleted in ^{13}C, indicating higher fraction of woody cover, with the exception of the period ca. 1.7–1.5 Ma. The PDFs indicate a very broad overall trend from more open environments ca. 6 Ma to more wooded ca. 3–4 Ma and back to more open after 2 Ma (The PDF figure is adapted from Cerling et al. (2011), and all data were obtained from the compilation by Levin (2013))

(Cerling et al. 1988). The $\delta^{13}C$ sequences for the Turkana basin shown in Fig. 2a illustrate the highly variable nature of the data, even for each place and period. As the Turkana Basin/Omo sequence is well dated and rich in pedogenic carbonate $\delta^{13}C$ data, Cerling et al. (2011) were able to invert the interpretation to produce, instead of an index of C_4 biomass, rather an index for woody cover, or a "paleoshade" proxy. This was achieved by quantifying the fraction of woody cover from a suite of modern tropical ecosystems from $\delta^{13}C$ of soil organic matter. In this system, "forest" is defined as having continuous tree canopy cover (≥ 80 % cover), "woodland/bushland/thicket/shrubland" contains 40 % of tall woody or bushy cover, "wooded grassland" comprises 10–40 % woody cover, while "grassland" represents grass/herblands with ≤ 10 % woody cover. After transformation for application to carbonates, the fossil pedogenic isotope data are represented as probability density functions (PDF) for each temporal bin in the Awash Valley and Omo-Turkana Basin sequences (shown in Fig. 2b). The results show that woody cover at these sites was for the most part lower than 40 % throughout the 6 Ma timespan, pointing to frequency of open environments at most of the associated hominin fossil sites (Fig. 2b). They also suggest that there is little evidence for a long-term trend toward progressively more open environments, as the data for 6.4 Ma shows less woody cover and more open environments than occurs even after 2 Ma.

A number of isotopic datasets now available for Miocene, Pliocene, and Pleistocene faunas from eastern Africa, Central Africa, and southern Africa also suggest that even after C_4 grasses had become well established, the proportions of C_4 (grass) over C_3 (browse, fruits, herbs, some underground storage organs) resources for fauna did not necessarily increase steadily, but fluctuated. However, because families adopted C_4 resources at different times, it is more difficult to discern proportional plant functional group patterns unless the data are reduced. In order to produce a taxon-free "C_3/C_4" index (following Sponheimer and Lee-Thorp 2003; Lee-Thorp et al. 2007), the frequencies of C_3, C_4, and mixed feeders were calculated for selected sites where several time periods are represented by faunal $\delta^{13}C$ data. The underlying idea is that browsers/frugivores will be favored in a closed habitat with significant tree cover, while grazers will be favored in open, grassy landscapes (Sponheimer and Lee-Thorp 2003). The results (Fig. 3) show considerable variability, at least partly due to the nature of the faunal assemblages. The Central African Chad data stand out with high proportions of C_4 feeders in all sites (Zazzo et al. 2000), suggesting significant open grassy vegetation from the Late Miocene through the Pliocene. This is hardly surprising given the setting alongside a fluctuating Paleolake Chad. Where sufficient $\delta^{13}C$ data is available for the Upper Miocene, as for the Turkana region (Uno et al. 2011) and to a lesser extent in the Tugen Hills (Roche et al. 2013) example shown (where several formations are "lumped"), it is apparent that even at that early stage, shifts occur from earlier open/grassy to more closed environments (Fig. 3). Among the South African hominin sites, the results suggest that the most significant shift toward more open, grassier landscapes occurred ca. 1.7 Ma (Fig. 3 lower panel), consistent with the eastern African Pleistocene data.

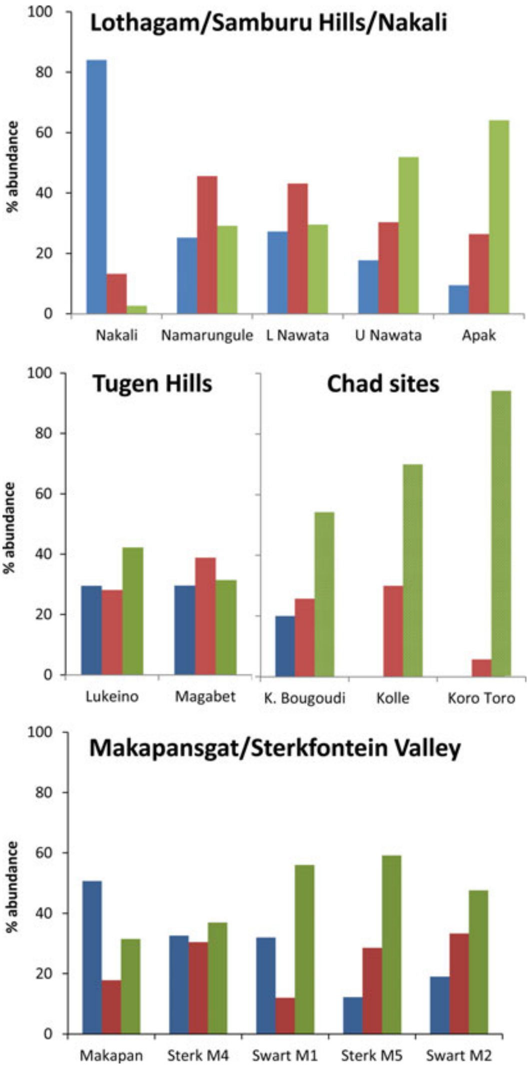

Fig. 3 The taxon-free C_3/C_4 index shown for a variety of sites in eastern and southern Africa for which sufficient data were available. Tooth enamel $\delta^{13}C$ data are reduced according to bins and shown as frequency diagrams, without regard to family, genus, or species, in contrast to the original version (Sponheimer and Lee-Thorp 2003) that used only Bovidae. The bins represent habitual C_3 feeders ($\delta^{13}C$ below −8 ‰), mixed feeders ($\delta^{13}C$ −7.9 to −3 ‰), and habitual C_4 feeders ($\delta^{13}C$ above/more positive than −2.9 ‰). The sites are, from *top*, the Lothagam Samburu Hills/Nawata sequence (Data from supplementary information in Uno et al. 2011), *middle*, the Tugen Hills sequence (Data from Roche et al. 2013) and the Chad sequence (Zazzo et al. 2000), and *below* a composite from the South African hominin sites of Makapansgat, Sterkfontein, and Swartkrans (From Lee-Thorp et al. 2007)

In some cases, faunal isotope $\delta^{13}C$ data apparently run counter to the perspective afforded by pedogenic carbonates, or to faunal abundances. For instance, de Heinzelin et al. (1999) suggest a wooded environment at ~2.5 Ma in the Awash, Ethiopia, based on soil isotope values, but faunal $\delta^{13}C$ data suggest a significant proportion of C_4 grazers (Levin et al. 2004). Pickford and Senut (2001) reconstructed the Tugen Hills environment in the Late Miocene and Early Pliocene to have been mostly forest, based on the presence of the closed habitat preferences of some of the fauna, but Roche et al. (2013) showed that at least for the Lukeino Formation C_4 feeders are more common in the faunal assemblage. A similar situation occurs in relation to environments associated with *Ardipithecus* sites in

Ethiopia, where arboreal or forest loving faunal elements indicated closed-canopy forest or woodland at Aramis (White et al. 2009), while $\delta^{13}C$ analyses at Gona also associated with *Ardipithecus* suggested high proportions of animals reliant on C_4 vegetation (Levin et al. 2008), but these apparent discordances may relate simply to scale and suggest that different parts of the ecosystem are being sampled.

The pedogenic carbonate and faunal $\delta^{13}C$ data, although informative about vegetation trends, are nevertheless constrained by relatively crude chronologies using large time bins. Two isotope proxies offer a means to discern shifts at much higher resolution – speleothems and plant wax biomarkers from lake sediments.

A large flowstone in Buffalo Cave, in the Makapans Valley, South Africa, provides highly resolved $\delta^{13}C$ and $\delta^{18}O$ data, yielding information about vegetation change and hydrology in the period between 1.95 and 1.5 Ma (Hopley et al. 2007). Variation in the $\delta^{13}C$ vegetation sequence is dominated by the obliquity cycle and in the $\delta^{18}O$ hydrology sequence by the precessional cycle. The sequence captures the shift to higher proportions of C_4 plants at 1.7 Ma, but, importantly, it shows that this change forms part of a series of orbitally controlled cycles. The differences in dominant orbital forcing modes for the two proxies emphasize the complexities of climate and environment and the need for multiple sources of evidence.

A different approach to obtaining high-resolution proxy information has been obtained from Olduvai paleolake sediments between 1.8 and 2.0 Ma, using $\delta^{13}C$ and δH signatures for lipid biomarkers extracted from lake sediment organic matter (Magill et al. 2013a, b). Isotope values for the leaf-derived wax biomarker (nC_{31}) are used to deduce the nature of terrestrial plant functional groups (forest to open vegetation) and the climate influences (rainfall amount, relative humidity) acting on them, while the algal biomarker (nC_{17}) reflects rather conditions related to hydrological conditions in the lake. Using published data for modern plants and soils in East Africa, the authors first constructed a framework for interpretation of ancient biomarker $\delta^{13}C$ and δD signatures. The ancient biomarker results show, firstly, that the proportions of closed versus open vegetation, and precipitation, are correlated. This observation is consistent with the Sankaran et al. (2005) modern survey. Secondly, leaf wax $\delta^{13}C$ indicates multiple recurring ecosystem shifts, from open C_4-dominated grasslands to more closed tree-dominated systems. Thirdly, these changes occurred on rapid timescales, within centennial or millennial scales. Unlike the Buffalo Cave record, the $\delta^{13}C$ (vegetation) shifts are correlated with the precessional cycle. These data provide a far more nuanced, detailed view of environmental and climate evolution, compared to the grosser scales provided by, for instance, pedogenic carbonates. They suggest, again, that the long-held inferences about stepwise aridification and opening of East African landscapes are incorrect. In some degree this may be a question of scale, but additionally the nature of links between savannas and precipitation has been poorly understood.

What does the floral information tell us of relevance to hominin evolution? For one, disputes remain about whether locally environments remained relatively closed versus open, as deduced from, say, faunal abundances. In combination these results suggest that in order to make these inferences, we need to base them on multiple sources of information, and certainly including isotopic data.

Despite the orbitally controlled variability shown in the more detailed sequences from Olduvai Paleolake and Buffalo Cave, the appearance of more open, grassy habitats around 1.7–1.8 Ma seems to have been pervasive in both eastern and southern Africa. Given the increasing evidence for presence of a fully bipedal, larger-brained, better technologically equipped hominin at this time, one is tempted to draw links between these two occurrences – habitual use, perhaps, of more open, more strongly seasonal, and exposed open environments with their own set of resource opportunities. Finally, the evidence for cyclical woody/open shifts requires reappraisal of previous interpretations of long-term trends. These new sequential data suggest that our view has been colored by the nature of the proxies available. Most of the existing data relies on material which may, in principle, reflect small time windows, but the time bins are quite gross. As a result, only large-scale environmental trends emerged. Yet the more rapid shifts visible in the biomarker and speleothem data are on a scale that must have impacted on resource and foraging opportunities of early hominins.

Aridity Indices From Oxygen Isotopes

Africa did not experience glaciation and large temperature swings associated with the glacial to interglacial shifts at higher latitudes. The climate variable of most importance and influence is undoubtedly rainfall, and thus there have been many attempts to capture this relatively elusive property. For many years, the perception has existed of an overall aridification trend based on observed trends toward more open, grassier African landscapes over the last ca. 5 Ma. As discussed above, however, grassy presence or dominance does not show such a trend when the entire sequence from the Upper Miocene is considered. Additionally C_4 presence is not an indication of aridity per se, although these grasses are successful in environments with relatively low rainfall. Canopy cover has been shown to be directly and more tightly correlated with mean annual precipitation (Sankaran et al. 2005), so it is likely a better indication of humidity. Given the difficulties of directly linking precipitation or aridity and vegetation cover (with some notable exceptions), it is important to explore multiple indicators to achieve this goal.

Wynn (2004) developed a new application of the pedogenic carbonate record, applying an empirical relationship of the "calcic depth" at which paleosol carbonates form and mean annual precipitation (MAP) derived from modern observations. In this relationship increasingly shallow calcic depth is associated with lower rainfall. Application to those sections of the existing Turkana Basin record (Wynn 2000) where calcic depth can be determined, at various noncontinuous intervals from 4.3 Ma, shows that prior to 2.5 Ma, calcic depth is greater, giving MAP estimates of about 600 mm/a. There follows an estimated decrease in MAP, interrupted by more humid conditions near 1.8 Ma. Interestingly, higher C_4 composition is not necessarily correlated with indications for higher aridity. Wynn (2004) points out that several extended intervals, dating to 4–3.6, 3.4–2.5, and 2.2–1.9 Ma, respectively, lack sufficiently developed carbonates to determine depth in spite of indications of sufficient humidity for soil development. Thus, it seems that the calcic horizon/MAP index is capturing only part of rainfall history.

Two recently proposed aridity indexes exploit the effects of relative humidity on evapotranspiration in plants and hence on the animals that rely on them to a greater or lesser extent. The first exploits the effects of relative humidity on plants and then fauna, using $\delta^{18}O$ differences between animals that use environmental water more directly (termed evaporation sensitive or ES) and those that rely mostly on plant water (termed evaporation insensitive or EI) (Levin et al. 2006). The isotopic difference between a suite of modern ES and EI taxa was found to correlate with a water deficit function for the site. Although the isotopic difference ($\varepsilon_{ES\text{-}EI}$) differs in absolute value for different pairs of ES and EI taxa, the slope of the relationship to water deficit remains relatively consistent. So far the relationship has been sparsely applied. Results for the Middle Pleistocene Asbole fauna, in the lower Awash Valley, Ethiopia, show that the ^{18}O enrichment between ES and EI taxa provides an estimate of a mean annual water deficit of 1,470 mm for the period ca. 0.8 Ma (Bedaso et al. 2010). This value is similar to that found in the area today. The advantage of this approach is that it is independent of $\delta^{18}O_{mw}$ values, but to obtain some meaningful idea of shifts in aridity over time requires extensive application to fossil faunas. This has not yet occurred.

An ostrich or ratite eggshell $\delta^{18}O$ aridity index is also ultimately reliant on relative humidity effects on plants. Ratite eggshell is ubiquitous in many arid archaeological and paleontological sites, and ostriches are known as arid-adapted birds that inhabit dry areas. Thus, the $\delta^{18}O$ composition of their eggshells provides a relatively direct indication of aridity. Data from modern and Late Pleistocene-Holocene archaeological sites show that eggshell $\delta^{18}O$ is correlated with mean annual rainfall and strongly with relative humidity (Lee-Thorp and Talma 2000; Lee-Thorp and Ségalen Unpublished Data). Ostriches rely primarily on plant and recycled metabolic water (Williams et al. 1993), so body water and eggshell $\delta^{18}O$ is strongly influenced by the effects of decreasing relative humidity on plant evapotranspiration. Eggshell $\delta^{18}O$ has been used to show high but fluctuating aridity levels in the Namib, from the Miocene through to the present (Ségalen et al. 2006). In this sequence the main constraint is chronology, as it is based on biostratigraphy and thus provides only crude time intervals.

Warm temperatures contribute to aridity because it promotes evaporation and reduces relative humidity levels. It has been suggested that conditions in East Africa were cooler in the Pliocene, along with being more densely wooded. Temperature has been difficult to assess independently but a new application of “clumped isotopes” that utilizes the distribution of ^{13}C–^{18}O bonds in pedogenic carbonates provides a means for estimating soil temperatures (Passey et al. 2010). The results for carbonates in the Turkana Basin, Kenya, show that the region has been not just warm, but hot, for the past 4 Ma (Passey et al. 2010). Estimated daytime soil temperatures regularly reached well above 30 °C, similar to temperatures in the region today.

Other than estimation of moisture or relative humidity, it is also useful to understand possible shifts in atmospheric circulation in the evolution of climate.

One variable is the dominant moisture source, since it has broader implications for atmospheric circulation. The Turkana Basin pedogenic carbonate $\delta^{18}O$ sequence strongly suggests that a significant change in vapor source or transport occurred in East Africa around 1.8 Ma. $\delta^{18}O$ values prior to this time were more negative, and thereafter significantly more positive. The most likely explanation is a shift in dominant vapor source from a distant one, likely the Atlantic Ocean, to a closer source, likely the Indian Ocean. $\delta^{18}O$ values for the latter period are sufficiently high to suggest that evaporation also exerted an influence on $\delta^{18}O$ as they do today. This data thus provides hints about atmospheric circulation, but little direct information about humidity or aridity.

Conclusions

In this chapter we have attempted to place some of the long-standing questions about the possible linkages between hominin evolution and environmental changes in an isotopic context, and on a sound footing. A number of principles and constraints must be considered for application of isotopic methods to paleoenvironmental questions, or the results are of limited value. In doing so we may have overemphasized the problems and constraints. So, in our concluding remarks we would like to emphasize some of the solid advances that have been made over the last couple of decades.

A great strength of isotopic approaches to paleoenvironments clearly lies in the area of delineating and quantifying vegetation changes, most particularly the presence and proportions of C_4 grasses in the plant biomass or, conversely, woody canopy. There are a couple of relatively minor discordances evident from some of the pedogenic carbonate compared to faunal enamel approaches, but in general the sequence of events is reasonably clear. The emergence of C_4 grasses as a significant part of the vegetation has been pushed back to 9 Ma ago in the low latitudes of Africa. According to the well-dated Samburu Hills/Turkana Basin sequences, this occurred quite rapidly, judging by the rapidity with which equids switched to C_4 plants. Although the data from southern Africa are far more fragmentary, they suggest that this floral shift took place rather later. After the initial major shift to C_4 grasses and sedges (as the evolution of C_4 photosynthesis also occurred in sedges at around the same time or perhaps earlier), these plant groups remained a significant component of the vegetation for millions of years. Taking the full faunal and soil carbonate isotope sequence into account shows that there was no progression toward more and more open environments. Rather there were continual shifts in the proportions of woody and grassy vegetation, varying spatially and on different timescales.

Among the larger-scale vegetation fluctuations, the shift around 1.8 Ma to more extensive grasslands stands out, since it occurred concurrently in both eastern and southern Africa. It may coincide with the emergence of the modern Walker Cell atmospheric circulation, so some of the circulation effects may have included more marked rainy and dry seasons. It is at this point that we see the birth of a "modern world," complete with vegetation and faunal distributions, and variable wet and dry seasons that we associate with "typical" African savanna environments.

At the same time, new high-resolution biomarker and speleothem isotope data point to the inherently cyclical nature of environmental change, at various scales, for both vegetation composition and rainfall. These data demonstrate that orbital forcing of African rainfall, with its strong implications for tree canopy cover, has considerable time depth. This is consistent with interpretations of the Saharan dust cycles (deMenocal 2004, 2011), which effectively indicate the converse, arid components of the system. Other than the still-rare lake biomarker and speleothem sequences discussed above, isotopic evidence for aridity or humidity and any trends in these features is still thin. However, significant advances have been made in developing new methods to address them.

We can use the isotopic data to evaluate the idea of a large climate-driven radiation about 2.4–2.8 Ma ago, as suggested in the "turnover-pulse" hypothesis (Vrba 1985). The evidence from $\delta^{13}C$ in fauna and pedogenic carbonates from East and South Africa suggests that, after the first explosion of C_4 vegetation about 7–9 Ma ago, the most significant biomass change to open, grassy ecosystems occurred near 1.8 Ma. It is tempting, but nevertheless speculative, to suggest that the emergence and success of a habitual, fully bipedal, well-equipped hominin, viz. *Homo ergaster*, is in some way connected with this significant environmental change. The nature of much of the isotopic evidence produced so far does not permit a detailed test of the "climate variability" hypothesis (Potts 1996), but high-resolution sequence data such as developed for the Olduvai paleolake may at last provide an appropriate means to do just that. This is because most data represents large chunks of time, and shorter periodicity is hidden. The new highly resolved lake sediment biomarker approach promises to break this impasse for the first time, although the possible locations for such studies are more limited than the coarser paleosol and faunal approaches. High-resolution speleothem isotope data are an equally promising archive, but are even more restricted in time and space, limiting their application and impact.

What can these shifts and large- and small-scale cycles tell us about hominin adaptations and evolutionary pathways? Are these issues linked, and if so, how? As noted above the "savanna hypothesis" ceased to be popular some time ago because the emergence of older dates for evolution of bipedalism was pushed back in time to periods in which canopied forests dominated the landscapes occupied by early hominins. Or so it appeared. Greater attention to the timing and interpretation of the paleosol carbonate and faunal isotope data suggest rather that open landscapes dominated for millions of years. It is also apparent that vegetation cover and humidity varied on relatively shorter timescales as well. These are scales that perhaps carried greater significance for hominin adaptation. Additionally we now know that hominins began to exploit C_4 resources from a relatively early stage (at least after 4 Ma) (Sponheimer et al. 2013). The implication is that when C_4 food resources became available, hominins often chose to make use of them, while our closest living relatives did not. Thus, it might be time to rethink the relationship between hominin evolutionary trends and the emergence of "savanna" landscapes yet again.

Cross-References

- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ Paleosols
- ▶ Quaternary Deposits and Paleosites
- ▶ Quaternary Geology and Paleoenvironments
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ The Biotic Environments of the Late Miocene Hominoids
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

John Rowan and Kaye E. Reed

Contents

Abstract

New evidence from relatively recent methodological advances into hominin autecology presents interesting and often contradictory data. This article presents a broad overview of various paleoecological methods and summarizes what is known about the paleoecology of late Miocene hominins, through the hominin genera that begin to appear in the early Pleistocene, ~2.0 Ma. The use of taxon-free methods is emphasized in elucidating hominin habitats, and a more careful consideration of taphonomic and depositional biases that often result in "mosaic" reconstructions is advocated. Methods that focus on understanding the behavioral ecology of early hominin and other mammalian taxa are reviewed.

J. Rowan (✉) • K.E. Reed
School of Human Evolution and Social Change, Institute of Human Origins, Arizona State University, Tempe, AZ, USA
e-mail: john.rowan@asu.edu; kaye.reed@asu.edu; kreed.iho@asu.edu

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Introduction

Paleoecology is concerned with understanding the ecology of organisms from the past, inasmuch as ecology can be reconstructed using the available evidence. The paleoecological evidence, whether biotic or abiotic, is then often compared with modern ecological patterns and processes to arrive at an understanding of the fossil taxon, taxa, or habitats of interest. Ecological patterns can be discerned in the past, but the processes that caused those patterns must be inferred. These can then be compared with modern ecological studies, wherein hypotheses about the processes are developed from observed patterns and subsequently linked to processes. For example, there are several hypotheses of community assembly processes, i.e., understanding why particular taxa co-occur in a circumscribed area, and these continue to be tested today (e.g., Hubbell 2001; Chase et al. 2005; Salisbury et al. 2012). There are many areas of inquiry that fall under the paleoecology rubric, including, but not limited to, geological depositional environments and paleosol analysis, habitat reconstruction, climate modeling, taphonomy, community ecology, biogeography, and autecology.

This chapter briefly outlines a variety of paleoecological methods that are used currently to develop reconstructions of the past habitat, climate, and behaviors of early hominins. What is currently known about early hominin ecology is synthesized, and those taxa recovered from the late Miocene, beginning at ~7 million years ago (Ma) to the end of the Pliocene, ~2.5 Ma, are included (Table 1).

Table 1 Habitat and dietary data for early hominin taxa

Taxon	Habitat	Isotopes	Microwear	References
Sahelanthropus tchadensis	savanna with some woody cover; semi-desert?	_	_	(Vignaud et al. 2002; Le Fur et al. 2009; Blondel et al. 2010)
Orrorin tugenensis	Forest-woodland mosaic	_	_	(Pickford and Senut 2001)
Ardipithecus kadabba	Riparian woodland	_	_	(Su et al. 2009)
Ardipithecus ramidus	Predominantly woodland; possibly bushland-grassland	C_3 dominated	_	(White et al. 2009; Louchart et al. 2009; Cerling et al. 2011a)
Australopithecus anamensis	Woodland; Woodland with gallery forests	C_3 dominated	Low complexity and anisotropy values; soft foods	(Leakey et al. 1995; White et al. 2006)

(*continued*)

Table 1 (continued)

Taxon	Habitat	Isotopes	Microwear	References
Australopithecus afarensis	Habitat generalist: riparian forest through bushland	Eurytopic; Individuals range from predominantly C_3 to predominantly C_4	Low complexity and anisotropy values; soft foods	(Reed 2008; Ungar and Sponheimer 2011; Wynn et al. 2013; Behrensmeyer and Reed 2013)
Australopithecus bahrelghazali	Grassland around lake margins	Predominantly C_4	–	(Brunet et al. 1996; Lee-Thorp et al. 2012)
Australopithecus africanus	Riparian woodlands, edaphic grasslands, dense to open woodland, and bushland	C_3/C_4 mixed feeder	Low complexity and anisotropy values; soft foods	(Reed 1997; Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005)
Australopithecus garhi	Grassland around lake margins	–	–	(Asfaw et al. 1999; de Heinzelin et al. 1999)
Australopithecus sediba	Grassland to woodland	Predominantly C_3	Moderate anisotropy, high complexity; some hard-object feeding	(Dirks et al. 2010; Henry et al. 2012)
Paranthropus aethiopicus	Wooded and wet in the Omo; dry and arid in the Ndolanya Beds, Laetoli	Predominantly C_4	–	(Bobe and Eck 2001; Harrison 2011; Cerling et al. 2013)
Paranthropus robustus	Woodland and grassland near water sources	C_3/C_4 mixed feeder	Hard-object feeding as evinced by pitting?	(Reed 1997; Ungar and Sponheimer 2011)
Paranthropus boisei	Mesic woodlands near lakes; grasslands at Konso, Ethiopia	Predominantly C_4	Low complexity and anisotropy values; soft foods	(Cerling et al. 2011b, 2013; Ungar and Sponheimer 2011)

(*continued*)

Table 1 (continued)

Taxon	Habitat	Isotopes	Microwear	References
Kenyanthropus platyops	Woody, well-vegetated (although the Nachukui Formation is generally the most arid in Turkana Basin)	Eurytopic; Individuals range from predominantly C_3 to predominantly C_4	_	(Leakey et al. 2001; Cerling et al. 2013)
Homo habilis	Generally open and arid grasslands; possibly wooded environments	C_3/C_4 mixed feeder	Low complexity and anisotropy values; soft foods	(Bobe and Behrensmeyer 2004; Ungar et al. 2006; Cerling et al. 2013; Kovarovic et al. 2013)

The Paleoclimatic Record

Research interest in the links between climate, ecology, and macroevolution has led to the advent of various proxies for paleoclimate during the African Plio-Pleistocene. While fauna has been historically used (e.g., Vrba 1985), new methods have come to the forefront of paleoclimatic studies, including records of terrigenous dust in marine drilling cores (e.g., deMenocal 1995), stable isotope analysis of paleosols (e.g., Cerling et al. 2011a), and stable isotope analysis of plant leaf wax (Feakins et al. 2013).

Vrba (1985, 1995) explored the interplay between paleoclimate and macroevolution using the fossil record of African mammals, primarily bovids, and such studies led to the formulation of the turnover pulse hypothesis (i.e., faunas “turnover” in synchronous-like fashion as a response to perturbations of climate). She suggests that the radiation of cool and arid-adapted mammals over warm and moist-adapted mammals is evidence that Africa became increasingly cooler and more arid over the past 5 million years. Indeed, the origins of *Paranthropus* and *Homo* have been linked with the cooling event shortly after 2.8 Ma. Marine isotopic evidence (e.g., Zachos et al. 2001) also supports cooling in Africa during this time, along with intensification of glaciation at Northern Hemispheres.

Using records of continental dust derived from marine drilling projects in the Arabian Sea and Gulf of Aden, deMenocal (1995, 2004) has suggested three steplike increases in aridity, as evinced by an increase in dust, in East Africa over the last few million years. Dust production increased between 3.0–2.6 Ma, 1.8–1.6 Ma, and 1.2–0.8 Ma, all three of which are broadly consistent with periods of turnover in African faunas previously proposed by Vrba (1995).

Overall, it is clear that over the past 7 Ma in Africa, climate was becoming increasingly cooler, terrestrial ecosystems were becoming more arid, and the variability of climatic changes was becoming more dramatic. While various hypotheses have been proposed to explain key events in the human lineage (e.g., bipedalism and material technology), none is universally accepted although none are mutually exclusive. The remainder of this chapter will provide habitat descriptions for hominin species, but will refrain from speculating on the impetus for innovations in human evolution. For further reading, an in-depth review of paleoclimate and hypotheses regarding hominin evolution was recently provided by Potts (2013).

Paleoecological Methods

Faunas as Paleoenvironmental and Paleoecological Indicators

The remains of other fossil vertebrates, primarily mammals, have historically played a large role in the reconstruction of hominin habitats, and this method is still used today. The last few decades have witnessed a paradigm shift in paleoecology from taxon-based to taxon-free methods (i.e., analyses that do not rely on taxonomic or phylogenetic information). Traditional taxon-based methods, such as the relative abundance of grazing taxon x vs. browsing taxon y, rely on the assumption of taxonomic uniformitarianism. Under such an assumption it is supposed that fossil taxa share dietary and habitat preferences with their extant congeners and that these ecological traits can be used in paleoenvironmental reconstructions. This is problematic. For example, some lineages were diverse in the past and have only a single or few living representatives (e.g., *Theropithecus*), while others exhibit changes in their dietary ecology through time that would have been completely unforeseen under expectations of ecological continuity between fossil and extant taxa. For example, Bibi et al. (2012) recently showed that the suid *Kolpochoerus limnetes* and the tragelaphin bovid *Tragelaphus nakuae* from the Shungura Formation of southern Ethiopia increasingly consumed C_4-based resources after 2.8 Ma, despite showing little craniodental change through time. The result was unexpected for both species, as modern analogs (*Potamochoerus* spp. and *Tragelaphus* spp.) are typically found in closed habitats, and C_3 plant sources make up the majority of their diet (Harris and Cerling 2002; Kingdon and Hoffmann 2013). This variation through time in lineages should caution future researchers wishing to reconstruct habitats based solely on taxonomic grounds. Unfortunately, taxonomically based methods remain pervasive in the hominin literature (e.g., Reynolds and Kibii 2011).

Bovids (antelope and their kin) are the most common mammalian family used in habitat reconstructions of the East and South African Plio-Pleistocene and provide a good model to explore the assumption of taxonomic uniformitarianism. Persistently, the relative distribution of bovid tribes in fossil deposits has been used as a proxy in habitat reconstructions and paleoenvironmental studies for sites of the

African Plio-Pleistocene (e.g., Vrba 1980; Shipman and Harris 1988; Harris and Leakey 1993). This methodology is based on the principle of taxonomic uniformitarianism, an idea itself based on the two postulates that (1) living representatives of bovid tribes collectively exhibit generalizable ecological preferences and that (2) these tribal preferences can be extended to their fossil representatives. However, there are notable difficulties with both of these assumptions.

With regard to living species, although members of a tribe may seem to collectively exhibit preferences for a certain habitat, the generalization is usually imprecise and there are always exceptions. For example, the sable antelope *Hippotragus niger* deviates from Hippotragini's generalized preference for open and arid grassland to semidesert habitats by instead preferring woodland and ecotones in the miombo (miombo is the Swahili word for the genus *Brachystegia*) woodland zone of southeastern Africa (Estes 2013). In Botswana, the southern limit of the sable's range happens to be limited by an annual rainfall isohyet of 500 mm, while fellow hippotragins *Oryx* and *Addax* persist, respectively, in habitats that receive much less than 500 and 100 mm of annual rainfall (Estes 2013; Knight 2013; Newby 2013). Similarly, the eland *Tragelaphus oryx* abandons its tragelaphin "tribal preference" for habitats with substantial woody cover and is found in habitats ranging from Kalahari semidesert scrub through Serengeti grassland to high-altitude alpine moorland on Mt Kilimanjaro (Thouless 2013). Through these examples, and there are many more, it is evident that homogenizing various habitat preferences of particular species into oversimplified habitat preferences for extant tribes, and then extrapolating this single homogenized tribal preference to fossil species living millions of years ago, is problematic without further explanation.

While the presence or absence of particular tribes might be of some paleoenvironmental significance, for example, the absence of reduncins at Laetoli (which indicates the lack of wetlands, lakes, or rivers (Gentry 2011)), paleoenvironmental and habitat inferences based on tribal relative abundance are subject to distortion by preservational, taphonomic, collection, and identification biases. For example, assemblages accumulated in fluvial systems may contain animals from multiple habitat types that often result in a "mosaic" reconstruction of early hominin habitats. Similar weaknesses characterize assemblages accumulated by carnivore activity, such as the size of prey that is accumulated and the resulting bias eliminating various size classes of animals that would be used in a paleoecological analysis.

In light of these issues, there has been a recent movement in paleoecology towards taxon-free methods of ecological and environmental reconstruction, based on fossil mammal specimens that do not rely on taxonomic or phylogenetic information. Such methods include isotopic analysis of herbivore enamel (Sponheimer et al. 2003; Cerling et al. 2011), mesowear of molar teeth (Fortelius and Solounias 2000; Kaiser 2011), craniodental ecomorphology (Spencer 1997), and postcranial ecomorphology (DeGusta and Vrba 2003, 2005a, b; Plummer and Bishop 1994). These taxon-free methods are used to re-create patterns of habitat use in mammals that existed with the early hominin taxa. Thus, the isotopic analysis of ungulate teeth from a particular site should provide an indication of the overall habitat from which the animals derived. Mesowear, craniodental, and postcranial ecomorphology provide the same types of patterns, although an improved pattern is developed if all of the methods are used and compared at one locality as this may identify taphonomic biases in the information. Since many hominin habitats have been reconstructed on taxonomic grounds, the evidence is included here, but strong conclusions based on these data are not possible.

Dental Microwear

Microscopic examination of the enamel surfaces of molars and incisors provides data in the form of scratches and pits on the teeth that can be used to infer what members of a fossil taxon were actually eating. Microwear has been utilized to understand the diet of hyraxes, bovids, monkeys, carnivores, and hominins (e.g., Walker et al. 1978; Grine and Kay 1988; Merceron et al. 2004; Scott et al. 2005; Ungar et al. 2008, 2010b). Traditionally, microwear has been assumed to exhibit scratches on the teeth caused by ingestion of food in the last weeks of the animal's life (Teaford 1988). Recently, however, Lucas et al. (2013) have called this into question. They suggest that what the microwear is measuring is grit, since other foodstuffs do not, in an experimental setting, mar teeth to the extent that dirt does. This obviously needs further investigation, but considering these claims it is remarkable that browsing bovid teeth and grazing bovid teeth, as evinced by extant samples, show consistent differences between these groups (e.g., Schubert et al. 2006). This analysis of diagnostic wear patterns can be extended to primates, as monkeys that eat hard seeds and nuts show pitting on their teeth, while those that eat soft and abrasive foods do not. The results of microwear analyses of hominin taxa are included as paleobiological data in the section on hominin taxa, as are some interesting problems that arise when comparing these analyses with other methods of reconstructing hominin diets, such as stable isotope analysis.

Isotopes in Paleoecology

Of all skeletal tissues, dental enamel is ideal for isotopic studies because it is more highly mineralized than bone, and is thus unlikely to undergo postdepositional chemical alterations (i.e., diagenetic changes), and because changes in diet throughout ontogeny can be investigated since enamel is an incremental tissue (Ungar and Sponheimer 2011). For dietary information ^{13}C is the most suitable isotope for inferring the feeding ecology of extinct taxa, as its composition is directly related to the physiology and isotopic composition of the plants from which it was derived. Different terrestrial plants use different photosynthetic pathways, and this is reflected in their ^{12}C and ^{13}C ratios; these ratios are of interest to paleoecologists because, depending on which species of plant are consumed, a diagnostic ratio becomes incorporated into the enamel of herbivorous mammalian taxa. In tropical environments like Africa, browse vegetation such as woody trees, forbs, and shrubs exhibit the signature of a C_3 photosynthetic pathway. Conversely, savanna and tropical grasslands are associated with a C_4 photosynthetic pathway. As previously stated, enamel has very low rates of diagenetic alteration and has proven to be a useful indicator for distinguishing between modern and fossil browsing (e.g., *Giraffa* spp.) and grazing species (e.g., *Equus* spp.). Quantitatively, browsers show ^{13}C values of $-8^0/_{00}$ to $-10^0/_{00}$, while grazers exhibit values greater than $-2^0/_{00}$ to $1^0/_{00}$. As would be expected, mixed feeders are characterized by intermediate values.

Stable isotopes of oxygen are useful for interpreting climatic conditions, as ^{18}O composition in organisms is largely determined by the ^{18}O composition of local drinking water (thus presenting a snapshot of altitude, aridity, precipitation, etc.). However, interpreting the results of stable isotope analyses of oxygen is confounded by the fact that organismal physiology and diet also influence oxygen ratios in mammals and must be taken into account when drawing conclusions from data. With mammals in particular, ^{18}O is strongly influenced by drinking behavior. Depleted levels of ^{18}O are observed in aquatic taxa and higher levels of ^{18}O are common in C_4-adapted and arid taxa.

Carbon isotopes can also be used in chemical analyses of paleosols, if there are carbonate nodules (Cerling and Hay 1986; Sikes 1994; Wynn 2000). These nodules usually form under drying conditions and can give representation of the percentages of grasses and dicots (bushes and shrubs) that were present when the soil was formed. In addition, the soil carbon and carbonates can be used to estimate carbon dioxide in the atmosphere, which enables a better understanding of the paleoclimate (Cerling 1992).

Recently, Cerling and colleagues (2011a) have developed a method using soil carbon isotopes to evaluate the percentage of woody cover that was present on the landscape when the paleosols were formed. The percentage of woody cover is based on the amount of shrubs, bushes, and trees that had the C_3 pathway in the paleosol. The woody cover method is especially important in reconstructing environments for ancient African landscapes, as most hominin fossil localities in eastern and southern Africa are believed to have been deposited under "savanna environments." A savanna is defined as having various amounts of woody cover (C_3) from 80 % to 20 % (Pratt and Gwynne 1977), with grasses (C_4) as ground cover. Reconstructions of past habitats and, in particular, hominin sites have suffered from the inaccuracy of the term "savanna" to describe what the habitat looked like, and indeed many people think of open grassland when they hear the term savanna, although 20 % woody cover is required. Cerling et al. (2011a) designed a formula to interpret exactly how much woody cover was present, although this method cannot differentiate between the types of woody cover. However, if methods are used in tandem a better depiction of the landscape is possible. For example, Cerling et al. (2011a) reconstruct the Dikika locality, where "Selam" was recovered, as a woodland, bushland, or shrubland, based on the fraction of woody cover. If one uses the fauna recovered from the Basal Member of the Hadar Formation to add to this interpretation, one would see many browsers and mixed feeders that independently indicate a bushland or medium density woodland. Using multiproxies to examine hominin ecology allows better understanding of the taxa and their relationship with their environments.

Finally, strontium isotopes have also been in play recently and have been used to investigate movement of hominin species on the landscape. Strontium isotopes are dependent upon the underlying composition of rocks and soil in any given area; for example, they have been used extensively in France to show that a particular wine grape was in fact grown in the area that is noted on a bottle of wine (Hodgkins 2012). In South Africa, Copeland et al. (2011) used these data to examine ranging patterns in early hominins and showed that the smaller hominins recovered in the Malmani dolomite region of South Africa had evidence of ingesting strontium outside of the range seen in that area. The authors suggested that this might reveal that male australopiths had relatively small home ranges and that females ranged widely. Thus, isotopic analyses permit inferences of social and reproductive behavior in the hominin fossil record.

Botanical Remains as Paleoenvironmental Indicators

Pollen, phytoliths, and wood have all been used to reconstruct the plant species that were present in ancient environments (Bonnefille and Riollet 1980; Bonnefille et al. 2004; Henry et al. 2011, 2012; Bamford 2005; Bamford et al. 2006). Fossilized plant material is subject to the same vagaries as fossilized animals, in that it is only preserved under certain conditions. Despite this, pollen has been recovered from many fossil localities, e.g., Hadar, Ethiopia, but only from particular strata, such as the Sidi Hakoma Tuff and in the base of the Denen Dora Member, and it has been noted that no pollen was preserved from the upper Kada Hadar Member. The conclusion is that reeds and grasses from the paleolake dominated Hadar, and through the section there were both increasing and decreasing proportions of tree and shrub species. Again, these data can be compared with the faunal data and isotope data, where available, to arrive at a better understanding of the habitat of *Australopithecus afarensis*. For example, there is a spike in the abundance of reduncin bovids at the beginning of the Denen Dora Member, indicative of lacustrine and wetland deposits that are consistent with the pollen data.

The analysis of fossil woods allows identification of the actual tree species that existed in the region, and this often helps in determining the types of woody cover and the habitat. Bamford et al. (2006) used both macro-plant fossils and phytoliths to refine the habitats from the broad vegetation reconstruction previously done. At the HWKEE (Henrietta Wilfrida Korongo East East) site, they determined that the region was first dominated by palm trees and then a mixture of palms, grasses, and other dicot plants.

Phytoliths have come into the forefront in analyzing hominin diets. Henry et al. (2012) noted phytoliths of various plant materials in the calculus of *Au. sediba*. These included a fruit phytolith and a bark phytolith, consistent with the C_3 diet reconstructed using isotopic data. Phytolith analyses like that of Henry et al. (2012) offer a promising avenue of research for reconstructing hominin autecology.

The Ecology of Hominin Taxa

Sahelanthropus tchadensis

The earliest potential hominin comes from ~6 to 7 Ma perilacustrine sediments in Toros-Menalla, northern Chad. TM 266-01-060-1, “Toumai,” is the holotype of *Sahelanthropus tchadensis*, a distorted cranium possessing a thick supraorbital torus, small canines, and a cranial capacity of about 360 cc. The site was biochronologically dated as apparently older than the Lukeino Formation fauna (ca. 6 Ma), and the Toros-Menalla assemblage appears most similar to the Lower Nawata fauna of Lothagam (ca. 5.2-7 Ma) (Brunet et al. 2002).

Over ten species of fish, and abundant hippopotamid and crocodile remains, suggest a large and permanent lake, in concordance with the depositional evidence. The terrestrial habitat was reconstructed as a mosaic ranging from savanna to gallery forests at the edge of the watercourses, along with floodplain environments. Evidence for desert or semidesert conditions within the mosaic comes from fossil sand dunes, proposed by the authors as the earliest evidence for desert conditions in the southern Sahara (Vignaud et al. 2002).

Savanna conditions at Toros-Menalla seem to have been more prevalent than previously proposed, since a recent analysis of bovid mesowear implies the presence of extensive grasslands and open environments (Blondel et al. 2010). The dominance of Hippotragini and Reduncini at Toros-Menalla is also suggestive of open expanses of herbaceous vegetation, as extant representatives of both tribes are typically grazers (Kingdon and Hoffmann 2013). Gerbils and ground squirrels, along with fossorial genera like *Orycteropus* and *Serengetilagus*, also indicate dry savanna environments (Le Fur et al. 2009).

No isotopes or microwear studies have been published on *Sahelanthropus*.

Orrorin tugenensis

Senut et al. (2001) erected the genus *Orrorin* for late Miocene hominoid remains from the Lukeino Formation in the Tugen Hills of Kenya dated 6–5.7 Ma (Pickford and Senut 2001; Sawada et al. 2002). The hominin status of *Orrorin* is mainly supported by the morphology of the proximal femur in BAR 1002’00 which suggests that it may have been a biped (e.g., Richmond and Jungers 2008); but this view is not unanimous (e.g., Wood and Harrison 2011). Pickford and Senut (2001) described the associated fauna, but no isotope or microwear analyses have been performed. The late Miocene habitat of *Orrorin tugenensis* was reconstructed as a woodland mosaic based on the predominance of *Aepyceros*, a genus whose extant representative prefers ecotones between light woodland and savanna (Fritz and Bourgarel 2013). Colobine monkeys were interpreted as evidence for the presence of forests in close proximity to the depositional center, which alternates between fluvial and lacustrine throughout the Lukeino sequence. Crocodiles, hippos, fish, and freshwater snails suggest large, permanent bodies of water.

Ardipithecus kadabba

Ardipithecus kadabba is a late Miocene species of hominin recovered from sediments along the western margin of the Middle Awash, Ethiopia (Haile-Selassie and WoldeGabriel 2009). The hominin-bearing Asa Koma and Kuseralee Members of the Adu-Asa Formation have been dated to 5.54–5.77 Ma and ca. 5.2 Ma, respectively (WoldeGabriel et al. 2009). Su and colleagues (2009) associated *Ar. kadabba* with a densely wooded and well-watered landscape characterized by riparian woodland. The Asa Koma and Kuseralee Members are particularly rich in reduncin bovids, and this was taken as evidence for edaphic grasslands or swampy areas on the landscape. In contrast, Levin et al. (2008) interpret the habitat of *Ar. kadabba* at Gona as being predominantly bushland-grassland, based on carbon isotopes from herbivore tooth enamel suggesting diets dominated by C_4 grasses. This implies some habitat flexibility for early *Ardipithecus*.

Ardipithecus ramidus

The early Pliocene hominin *Ardipithecus ramidus* is best known from Aramis, a locality in the Middle Awash region of Ethiopia. The Lower Aramis Member of the Sagantole Formation is bracketed by two marker tuffs that constrain the age of Aramis to 4.4 Ma. The depositional environment has been characterized as a low-relief aggrading floodplain. White and colleagues (2009) recently published a comprehensive synthesis of the Aramis paleoenvironment using various lines of evidence (e.g., taxonomic abundance, mesowear, isotopes), and it is thus no surprise that the paleoenvironment of *Ar. ramidus* is the most completely known for all of the late Miocene-early Pliocene hominin taxa. The habitat evidence from Aramis is consistent with woodland exhibiting grassy and closed patches (although see Cerling et al. 2011a).

Carbon isotopes for *Ardipithecus ramidus* reveal a diet primarily comprised of C_3 plant products. The oxygen isotope data for *Ardipithecus* are slightly lower than the Aramis monkeys, suggesting that *Ar. ramidus* "obtained more water from fruits, bulbs, tubers, animals, and/or surface sources" (White et al. 2009). Dental morphology is broadly consistent with the isotopic data and indicates that the diet of *Ardipithecus* was generally derived from forest and woodland components. Suwa et al. (2009) showed that the enamel thickness of *Ar. ramidus* is intermediate between *Pan* and *Australopithecus* and suggested that the combined evidence indicates generalized omnivory and frugivory.

The community composition at Aramis is particularly interesting, being dominated by tragelaphin bovids and colobine monkeys. Cercopithecids in general are strikingly common at Aramis, as specimens attributable to *Pliopapio alemui* and *Kuseracolobus aramisi* comprise 30 % of the large mammal fauna, with the latter being the most common monkey in the assemblage. Conversely, equids are rare although the *Eurygnathohippus* species present at Aramis appears to be postcranially adapted to open-county running. *Tragelaphus* is the most common bovid, comprising 85 % of all antelope specimens collected. *Aepyceros* is also relatively common at Aramis, while Alcelaphini and Hippotragini are uncommon. Parrots and the peafowl *Pavo* dominate the avifauna, and it was suggested by Louchart et al. (2009) that the relatively rare arid-adapted rodents of Aramis were transported by raptors, since woodland micromammals comprise most of the assemblage.

Ecomorphological analyses of postcrania investigated habitat-linked traits in cercopithecid and bovid specimens, almost all of which were classified as "forest." Mesowear analyses revealed browsing preferences for the Aramis giraffids, tragelaphins, and "neotragins," while *Aepyceros* fell closer to the grazing end of the spectrum. Enamel isotopes reveal that grazing taxa were relatively uncommon and that browsing taxa dominated the assemblage. Notably, most fossil mammals at Aramis conformed to dietary expectations based on their extant congeners, which, in this case, supports the validity of taxon-based methods (e.g., relative taxonomic abundance) used to reconstruct the paleoenvironment of *Ardipithecus* at Aramis. The analysis of White and colleagues (2009) is a model example of the use of taxon-based methods, once independent lines of evidence have confirmed the supposed ecologies of indicator taxa.

Australopithecus anamensis

Australopithecus anamensis is the first species in the genus *Australopithecus* and has been found in sites in both Ethiopia and Kenya, appearing at Kanapoi, Allia Bay, Fejej, Aramis, Asa Issie, and Galili in roughly contemporaneous sediments indicating an origin of *Australopithecus* about 4.2 Ma. At Asa Issie, *Au. anamensis* is found in a woodland environment (White et al. 2006), while Kanapoi and Allia Bay were reconstructed as woodland mosaics with extensive gallery forests (Leakey et al. 1995).

Like *Ardipithecus*, the carbon isotopes of *Au. anamensis* reveal a narrow and C_3-based diet (Cerling et al. 2013). White et al. (2006) hypothesized niche expansion in early *Australopithecus* as the dentognathic morphology of *Au. anamensis* is indicative of consumption of tough, abrasive food resources relative to earlier hominins like *Ardipithecus*. Microwear analyses of *Au. anamensis* are notably similar to its descendant *Au. afarensis*, suggesting some dietary continuity between the lineages, although the evidence from isotope data contradicts this (Ungar and Sponheimer 2011; Wynn et al. 2013).

Australopithecus afarensis

Australopithecus afarensis is the most completely known species of Pliocene hominin (Kimbel and Delezene 2009), likely due to its extensive geographic and temporal distribution. This species persists from roughly 3.8 to 2.95 Ma and is best documented by the well-constrained sediments in the Afar of Ethiopia and, to a lesser extent, the Upper Laetolil Beds of Laetoli, Tanzania (Harrison 2011). *Au. afarensis* is likely present 2,500 km west of the Rift Valley at Koro Toro, Chad (as *Au. bahrelghazali* sensu Brunet et al. 1996), but it is relatively rare in the Omo-Turkana Basin, represented by poorly preserved craniodental remains, despite the Basin's close proximity to other East African sites (e.g., Suwa et al. 1996; Kimbel 1988).

The earliest well-documented specimens of *Au. afarensis* come from the Upper Laetolil Beds of Laetoli, Tanzania. The paleoenvironment of Laetoli has been subject to debate. In the seminal 1987 volume on Laetoli edited by Mary Leakey and John Harris, most contributing authors concluded that past and present environments at Laetoli were effectively equal. This implied that the region must have been continuously characterized by savanna habitats, with some mixture of open woodland, since the mid-Pliocene when the Lower Laetolil Beds were deposited on bedrock. However, this view of habitat uniformity through time no longer appears to be true for Laetoli based on various lines of evidence including bovid ecomorphology (e.g., Kovarovic and Andrews 2007), vegetation structure (e.g., Andrews and Bamford 2008), and stable isotope analysis of herbivorous mammals (e.g., Kingston and Harrison 2007). These studies converge on the conclusion that Laetoli was wetter and more wooded during the deposition of the Laetolil Beds (3.8–3.5 Ma) than originally reconstructed. Ephemeral streams and ponds were likely present; however, the lack of aquatic taxa suggests permanent bodies of water were never present at Laetoli during this time. Hippopotamuses, crocodiles, and reduncin bovids are all absent from Laetoli, while they are common elsewhere in the East African Plio-Pleistocene. Despite this significant habitat difference, hominins are present at Laetoli and were probably more common than their relative abundance alone would suggest due to taphonomic biases related to body size (Su and Harrison 2008). Overall, the most recent data are in disagreement with original reconstructions of Laetoli, and the habitat of *Australopithecus afarensis* at Laetoli does not seem overtly anomalous with respect to other sites where the taxon is found, such as Hadar, which is discussed below.

The Hadar Formation of Hadar, Ethiopia, ca. 3.45–2.9 Ma, has produced the bulk of *Au. afarensis* specimens and permits longitudinal studies of this hominin's ecology since *Au. afarensis* is found throughout the entirety of the Hadar sequence (Campisano 2007). The paleoecology of the well-constrained Pliocene sediments at Hadar was recently reconstructed by Reed (2008). She provided habitat reconstructions for all members of the Hadar Formation by synthesizing faunal evidence with pollen and depositional data. In general, going up in the sequence, environments are wooded and closed during Sidi Hakoma times, transitioning to a wetter period in the Denen Dora when edaphic grasslands spread during the DD-2 submember and finally to more open and arid grasslands in the Kada Hadar Member (Reed 2008). *Au. afarensis* is most common in the Sidi Hakoma Member and, after declining in abundance, bounces back during the DD-2 submember when waterlogged grasslands dominate the landscape as evidenced by a substantial peak in reduncin bovids (Reed 2008). From the DD-2 submember on, the abundance of hominins stays relatively constant until they decline slightly in the KH-2 submember and then disappear from the Hadar fossil record roughly 2.95 Ma (Reed 2008; Kimbel and Delezene 2009). The evidence from Hadar supports the notion that *Australopithecus afarensis* was a habitat generalist as previously hypothesized (e.g., White et al. 1993).

Other habitat reconstructions are available for *Au. afarensis*. Woodland habitats dominate at Woranso-Mille, as the fauna is rich in Tragelaphini, *Aepyceros*, and *Theropithecus oswaldi* aff. *darti* (Geraads et al. 2009; Haile-Selassie et al. 2010). At Dikika, *Au. afarensis* is associated with woodlands around a delta, but grasslands may have also been present (Wynn et al. 2006). Two molars of *Au. afarensis* have been recovered from a Ledi-Geraru site sampling the Denen Dora Member of the Hadar Formation that contains numerous reduncins, alcelaphins, and antilopins suggestive of areas containing wet and dry grasslands. White et al. (1993) reconstructed the environment at Maka in the Middle Awash as woodland-bushland using faunal evidence.

Microwear studies of *Au. afarensis* have revealed a lack of pitting and low complexity values, i.e., no evidence for hard-object feeding (Grine et al. 2006), despite the general robusticity of *Au. afarensis* craniodental architecture (e.g., Rak et al. 2007). Carbon isotopes imply that *Au. afarensis* was a dietary eurytope, as individuals throughout the Hadar Formation were consuming both C_3 and C_4 resources, with the latter being more common (Wynn et al. 2013). The isotopic evidence for *Au. afarensis* has broader implications for hominin evolution, as the time period ~3.5 Ma seems to represent a dietary shift among hominins to C_4-based resources, at least partially, as this trend is also seen in contemporaneous Chadian *Australopithecus* and *Kenyanthropus* (Lee-Thorp et al. 2012; Cerling et al. 2013; Wynn et al. 2013). The proposition that *Au. afarensis* was using stone tools and consuming meat by 3.4 Ma at Dikika, as evinced by purported cutmarked bones (McPherron et al. 2010), requires further evidence.

Australopithecus bahrelghazali

Brunet and colleagues (1996) erected a new species of *Australopithecus*, *Au. bahrelghazali*, for a fragmentary hominin mandible recovered in ca. 3.5 Ma sediments at Koro Toro, Chad. The validity of *Au. bahrelghazali* has been called into question since the mandible shares strong similarity with *Au. afarensis*, known from contemporary sediments at Hadar, Ethiopia (White et al. 2000). The fauna at Koro Toro is similar to that of Hadar, sharing some common elements (e.g., *Kolpochoerus afarensis* and *Parmularius pachyceras*) and hinting at potential faunal exchange across north-central Africa during or before this time (Brunet et al. 1996; Geraads et al. 2001, 2012). Evidence from the Koro Toro bovids suggests open environments as Reduncini and Alcelaphini dominate, while Tragelaphini and *Aepyceros* are notably absent. The absence of other primate taxa at Koro Toro may also point to a lack of canopy cover on the landscape.

Isotopic evidence reveals *Au. bahrelghazali* was incorporating large amounts of C_4 foodstuffs in its diet ca. 3.5 Ma, as evinced by its significantly high ^{13}C values (Lee-Thorp et al. 2012). C_4 sedges with associated tubers and corms provide a potential explanation. The sedge genus *Cyperus* is widely distributed in tropical environments today and is often found around the margins of watercourses in Africa, including modern Lake Chad (White 1983; Lee-Thorp et al. 2012). It is possible that *Au. bahrelghazali* was exploiting sedges or similar plants around waterways, in a predominantly savanna environment. Thus, the dietary evidence would be in concordance with the faunally based habitat reconstruction and shows that Chadian *Australopithecus* lived and died in grasslands, suggestive of some degree of dietary and habitat flexibility in mid-Pliocene hominins considering that contemporaneous sites are typically wooded and well watered (e.g., Hadar).

Australopithecus africanus

Dart (1925) identified this taxon from the Taung mining dumps, and in the next several decades more individuals were discovered at the former cave sites of Sterkfontein and Makapansgat, although at first these hominins were referred to different species (Broom 1938; Dart 1958). Teeth were also recovered from the Gladysvale site in the 1990s (Berger and Tobias 1994). New paleomagnetic and uranium-lead dating of these cave sites suggests an age range of 3.0–2.0 Ma (Herries et al. 2013).

Habitat reconstructions differ for each of these sites. Makapansgat, considered the oldest of the localities, has been reconstructed as a mosaic of riparian woodlands, edaphic grasslands, and bushlands, with possible riverine forests (Dart 1925; Reed 1997). A study of bovid taxa, using both isotope values and ecomorphology of the masticatory apparatus, indicated that there were more browsing taxa than expected, and thus when the fauna was deposited, there may have been more closed woodland bushland than previously thought (Sponheimer et al. 1999). Taung has been reconstructed as dense woodland (Dart 1925; Berger and Clarke 1995); Sterkfontein has been reconstructed as open woodland, riparian forest, and bushland (Reed 1997; Clarke 2013). Finally, Gladysvale is considered to have ranged from closed to open vegetation (Berger and Tobias 1994).

Early works on both dental microwear and carbon isotopes were accomplished on this taxon. Grine (1986) and Grine and Kay (1988) suggested that the diet of *Au. africanus* was likely soft fruit and leaves, based on comparisons with chimpanzee microwear. However, later work on isotopes showed that this taxon had a very large range of carbon isotope values that included both C_3 and C_4 plants (Sponheimer and Lee-Thorp 1999; Sponheimer et al. 2005). Sponheimer et al. (2013) suggests that *Au. africanus* may have had greater population densities than forest-dwelling great apes due to their broad dietary patterns. Finally, Copeland et al. (2011) suggest that in *Au. africanus* females dispersed from their natal group, as evinced by strontium isotope analysis of the hominin teeth from Sterkfontein.

Australopithecus garhi

Australopithecus garhi is an enigmatic species of hominin known from a maxilla with complete dentition and postcranial remains from the Hata Member of Bouri, Ethiopia, ca. 2.5 Ma (Asfaw et al. 1999). The habitat of *Au. garhi* was reconstructed as grassy margins around a large freshwater lake, as evinced by high proportions of alcelaphin bovids and water-dependent taxa including hippos and crocodiles. If some Omo specimens are attributable to *Au. garhi*, as suggested by White (2002), this would place *Au. garhi* in a wetter and more heavily wooded environment than it is found in at Bouri (Bobe and Eck 2001; Bobe et al. 2007).

The remains of *Au. garhi* at Bouri are associated with zooarchaeological evidence for butchery and meat consumption. Cutmarks and percussion marks from stone tools were found on bovid and equid bones during the excavation of the BOU-VP-12/1 locality (de Heinzelin et al. 1999). The oldest stone tools occur at Gona about 2.6 Ma and are therefore roughly contemporaneous with the occurrence of cutmarked bones in the Hata Member (Semaw et al. 1997).

Australopithecus sediba

Discovered in August 2008 (Berger et al. 2010), this species appears to combine a more derived dentition with a primitive australopith body plan. Indeed, its generic attribution to *Australopithecus* was questioned during initial publication. Carbon isotopes indicate *Au. sediba* was feeding primarily on C_3 plant resources, and wood or bark has been suggested as a potential component of the diet, based on phytoliths recovered from dental calculus (Henry et al. 2013). It is interesting that *Au. sediba* incorporated no or very few C_4 food in its diet, as this is generally opposite the pattern observed in East Africa *Australopithecus*, with the exception of *Au. anamensis* (Sponheimer et al. 2013), although this may be an artifact of the small sample size of *Au. sediba*, as the Hadar hominins vary greatly in their isotopic signatures and thus the Malapa hominins could be sampling only the C_3-end of the spectrum.

Paranthropus aethiopicus

Arambourg and Coppens (1968) named a new species of hominin, *Paraustralopithecus aethiopicus*, and designated an edentulous mandible from Member C of the Shungura Formation as the holotype. The species was later realized to be the oldest member of the genus *Paranthropus* once the "Black Skull" KNM-WT 17000 was discovered (Walker et al. 1986).

The Omo habitat of *Paranthropus aethiopicus* was likely dry, closed, and wooded, since the lower part of the Shungura Formation shows a shift from wet woodlands in Member B to drier woodlands in Member C (Bobe and Eck 2001). *Paranthropus aethiopicus* has recently been reported from the Ndolanya Beds of Laetoli and is placed into the context of a savanna habitat with nearby woodland (Harrison 2011).

Cerling et al. (2013) found that Turkana Basin specimens of *P. aethiopicus* were characterized by diets high in C_4 content, as C_3 plant material comprised 50 % of the diet or less. Notably, 85 % of the diet of KNM-WT 17000 was found to derive from C_4 resources. This trend apparently continued in the eastern African *Paranthropus* lineage, as *P. boisei* typically exhibits the highest C_4 values of any hominin species for which we have isotopic data.

Paranthropus robustus

This taxon was discovered and named by Robert Broom (1938) at the Kromdraai mining site. Individuals have been recovered since that time at other cave locations in South Africa: Swartkrans, Drimolen, Gondolin, and Coopers D. Habitat reconstructions for these sites (except Drimolen) show them to be open woodland and grassland, although there always appears to be water in the form of rivers or wetlands in the vicinity as represented by the fauna (Brain 1993; Reed 1997; de Ruiter et al. 2009).

Robinson (1954) first suggested that *P. robustus* ate harder and different foodstuffs than *Au. africanus* because of the differences in the morphology of the masticatory apparatus in the two taxa. Grine (1986) tested this hypothesis by examining the microwear of both taxa, concluding that *P. robustus* had heavier pitting on its molars, and therefore a harder diet. Isotopic data suggest that this species ate a broad range of plant material ranging from trees and shrubs to grasses, i.e., C_3 and C_4. Strontium isotopes also suggest that the female of this species was the sex to leave the natal group, if the smaller teeth represent female individuals (Copeland et al. 2011). Finally, a study by Grine et al. (2012a) suggests that extremely large males of this species may be missing from the fossil record, as a large molar from Gondolin exceeds the size specifications of most other males. These researchers propose that taphonomic biases against these larger individuals have underestimated sexual dimorphism in this species.

Paranthropus boisei

The paleobiology of *Paranthropus boisei* has been the subject of debate since its initial description as *Zinjanthropus boisei* by Louis Leakey (1959). Consequently, more research has been devoted to the dietary and habitat preferences of *P. boisei* than to virtually any other hominin. Leakey dubbed OH 5 "nutcracker man" because of its dished and buttressed face, prominent sagittal crest, huge postcanine dentition, and nubby anterior teeth. Everything about the craniodental morphology of OH 5 seemed adapted for crushing hard, brittle food items with powerful jaw muscles, and this view persisted until relatively recently (e.g., Wood and Strait 2004).

P. boisei has been often linked with a closed and mesic habitat preference (Shipman and Harris 1988) although specimens of *P. boisei* from Konso in southern Ethiopia are associated with an arid grassland fauna (Suwa et al. 2003), similar to the habitat of *P. boisei*'s presumed ancestor *P. aethiopicus* in the Upper Ndolanya Beds of Laetoli (Harrison 2011). Reed (1997) found that *P. boisei* was found in more open environments and that *P. aethiopicus* was associated with closed habitats. At Olduvai, *P. boisei* specimens from Bed I and lower Bed II are associated with woodland environments, although habitats tend to appear wetter in the latter due to the presence of the Olduvai paleolake (Sikes 1994; Kovarovic et al. 2013).

The occlusal microwear of *Paranthropus boisei* is low in complexity and anisotropy values, similar to *Au. anamensis* and *Au. afarensis* (Ungar et al. 2008; Ungar and Sponheimer 2011). The evidence from microwear throws doubt on the title of *P. boisei* as "nutcracker man" and is instead suggestive of a frugivorous diet. Fallback hypotheses have been put forth to explain the discrepancy between the hyper-robust craniodental morphology of *P. boisei* and the evidence from microwear studies. Was *P. boisei* preferentially eating soft and fleshy food resources (i.e., fruits), only consuming harder and more brittle foods during times of resource stress? More evidence is needed, and the carbon isotope data make the story even more puzzling.

Cerling et al. (2011b) revealed that the vast majority of *P. boisei*'s diet was derived from C_4 plant sources, using carbon isotope analysis. *P. boisei* was also a highly water-dependent taxon as evinced by low $\delta^{18}O$ values, second only to *Hippopotamus* (Cerling et al. 2011b), throwing support behind mesic habitat reconstructions for the species. C_4 sedges are a potential food source based on the carbon and oxygen evidence, as sedges are often found around the perimeter of East African wetlands today and might also be characterized by relatively low $\delta^{18}O$ values as they are not subject to evapotranspiration pressures facing other terrestrial plant species (Lee-Thorp, 2011). Similarly, van der Merwe et al. (2008) hypothesized that *P. boisei* at Olduvai Gorge was consuming swampy C_4 vegetation, possibly papyrus.

Kenyanthropus platyops

Kenyanthropus platyops is a curious hominin of uncertain phylogenetic placement from mid-Pliocene sediments in West Turkana, Kenya (Leakey et al. 2001). High proportions of Alcelaphini and Antilopini in members of the Nachukui Formation in West Turkana suggest open and arid habitats throughout most of the sequence (Bobe et al. 2007). However, Leakey and colleagues (2001) reconstructed environments in localities LO4, LO5, LO6, and LO9 of the Lomekwi member as well vegetated and relatively wet in their initial publication of *Kenyanthropus platyops*. They report a high proportion of ecotonal (e.g., *Aepyceros*) and forest-dwelling (e.g., *Tragelaphus*) species relative to taxa of other bovid tribes. The synthetic picture of West Turkana during the mid-Pliocene emerges as relatively arid, with patches of woodland, while development of riverine forests was supported by small fluvial systems draining along the western margin of the basin (Leakey et al. 2001).

Carbon isotopes of *Kenyanthropus* dental specimens reveal a flexible diet similar to contemporaneous *Au. afarensis*, with diets spanning the C_3 to C_4 spectrum (Cerling et al. 2013).

Homo habilis

The Maka'amitalu Basin of Hadar is most notable for producing what is generally accepted as the earliest specimen of the genus *Homo*, a maxilla designated AL 666-1, with in situ Oldowan tools dated to 2.3 Ma (Kimbel et al. 1996). Earlier occurrences from Lake Baringo (ca. 2.3 Ma) and West Turkana (ca. 2.34 Ma) in Kenya have been proposed, but the evidence is fragmentary, consisting of a temporal bone and juvenile lower molar, respectively (Hill et al. 1992; Prat et al. 2005). The origin of the genus *Homo* has often been linked with environmental change, primarily in the form of increasing seasonality and aridification during the late Pliocene. It is thought that increasingly arid terrestrial environments and greater oscillations of climate imposed novel selective pressures on the human lineage during this time. For example, Bobe and Behrensmeyer (2004) note, "The fundamental importance of grasslands may lie in the complexity and heterogeneity they added to the range of habitats available to the early species of the genus *Homo*." Furthermore, Vrba (1985) proposed that an environmentally driven turnover in bovids between 2.7 and 2.5 Ma corresponded to the extinction of *Australopithecus* and the origin of *Homo* and *Paranthropus* in South Africa. Although savannas have been implicated as drivers for various events in human evolution (e.g., encephalization, toolmaking, and bipedalism), the expansion of grassland ecosystems in Africa has most often been implicated in the origin of *Homo*.

The paleoenvironment of AL 666-1 is under current study, but preliminary results suggest relatively open and arid conditions with the presence of nearby thickets or woodland. Conversely, Reed and Geraads (2012) reconstructed the Busidima Formation locality AL 894 as a woodland-to-forest habitat that was well watered based on a rodent assemblage dated to ca. 2.4 Ma. Given that these two sites are separated by nearly 100,000 years of time, the results are not mutually exclusive. Throughout East Africa, Reed (1997) showed that *Homo* is often associated taxa indicative of open and arid environments. The Olduvai record of *H. habilis* occurs in more heavily wooded environments and the presence of the Olduvai paleolake in lower Bed II provided a permanent water source (Kovarovic et al. 2013).

Specimens of early *Homo* from the Turkana Basin exhibit dietary breadth and were apparently consuming both C_3 and C_4 resources (Cerling et al. 2013).

Conclusions

In his description of the Taung Child, Raymond Dart proposed savannas were a driving force in human evolution, stating that "… a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution" (Dart 1925). Indeed, researchers have recognized the importance of environments in early human evolution ever since Darwin, traditionally focusing on the faunal context of hominin sites. Taxon-free methods like ecomorphology and isotopes have superseded such approaches and new methods are continually being developed, such as woody cover reconstructions based on carbon fractionation from paleosols (Cerling et al. 2011a).

The habitats of the earliest hominins are somewhat perplexing. Faunal evidence implies *Orrorin* existed in a forested habitat and both species of *Ardipithecus* are associated with fairly closed woodland habitats, while *Sahelanthropus* is purportedly associated with savanna and semidesert conditions along a lakeshore. The accumulating evidence for wooded habitat preferences during the early stages of human evolution is in stark contrast to decades of associating the origin of Hominini (and bipedalism) with the expansion of grasslands during the late Miocene. In contrast, Cerling et al. (2011a) recently resurrected the idea that savanna habitats played a large role throughout the course of human evolution and, in conjunction with growing dietary evidence, that some hominins shifted to C_4-dominated diets by 3.5 Ma.

Sites containing *Australopithecus* are often reconstructed as "mosaics," but this could be due to time averaging and depositional processes or actually represent various habitats across the landscape. *Au. afarensis* persists at Hadar despite various environmental changes throughout the Hadar Formation (Reed 2008). *Au. afarensis*, and possibly all of *Australopithecus* species, were habitat generalists. The isotopic evidence supports a broad diet for four of these taxa, if one considers that eating both C_3 and C_4 plants indicates something bordering on a generalist diet. While both *Au. anamensis* and *Au. sediba* appear to have consumed only C_3 plant material, the specifics of those C_3 foods are not known, and indeed an impressive range of plants and plant parts could have made them dietary generalists as well. The microwear evidence presents somewhat of a conundrum when these results are compared with the isotopic data in some species (Grine et al. 2012b; Ungar et al. 2010a). The South African taxa *Au. africanus* and *P. robustus* both exhibit variability in their dental microwear (Grine 1986) that matches the variation in C_3 and C_4 plant foods that they consumed, whereas the East African *Au. afarensis* exhibits extreme uniformity in the microwear scratches on teeth but included both plant types in its diet. It is possible that *Au. afarensis* ate the same types of foods, e.g., roots and tubers, from both C_3 and C_4 plants. In the future, if extraction of phytoliths from dental calculus in these species is possible, a better idea of the actual diet consumed may be available.

The impressive craniodental complex of *Paranthropus* is likely derived from an australopith ancestor ~2.6 Ma that began focusing on some different form of food. This is complicated further by the isotopic differences in the East and South African species. Repetitive loading, i.e., intensive chewing, could provide the adaptive explanation for such headgear. Conversely, various "fallback" explanations have been proposed to explain the discrepancy between microwear, isotopes, and the highly derived craniodental morphology of *Paranthropus* spp., but none is a particularly satisfying explanation. If the massive jaws of *Paranthropus* are in fact adaptations to fallback foods, then it seems likely that *P. robustus* engaged in this behavior more often than *P. boisei*, as the former exhibits pitting and high complexity values indicative of hard-object feeding (Ungar and Sponheimer 2011). As the jaws and teeth of *P. boisei* are even more robust, this is an obvious area for further study.

The role of environments in human evolution is as important as ever, and improving the accuracy of habitat reconstructions is critical as we delve deeper into the autecology of the earliest hominins with the refinement of microwear, isotopes, biomechanics, and other analyses. While it is true that most African habitats are somewhat mosaic in that they contain a diverse vegetation physiognomy, a more careful consideration of taphonomic and depositional biases, especially time averaging, is warranted. For faunal habitat reconstructions, the use of taxon-free methods (e.g., enamel isotopes) over taxon-based methods (e.g., tribal relative abundance) is encouraged because the latter involves considerable assumptions. In closing, while this chapter provided only a brief summary of methods and reconstructions of hominin habitats, the subject is worthy of a lengthier review. New methods are continually being developed and often contradict what we thought we knew about human evolution, and an in-depth synthesis of current lines of evidence would benefit all researchers in paleoanthropology.

Cross-References

- ▶ Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes

- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Paleosols
- ▶ Patterns of Diversification and Extinction
- ▶ Quaternary Deposits and Paleosites
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ The Biotic Environments of the Late Miocene Hominoids
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Geological Background of Early Hominid Sites in Africa

Ottmar Kullmer

Contents

Abstract

Hominid remains are rare elements in the fossil record. Probably, the small population sizes of early hominids, in combination with preservation constraints, limit any probability of a higher frequency of fossil discoveries. The early evolution of mankind appears to be a Pan-African story, even though the distribution pattern of remains concentrates on eastern and southern Africa. More recent findings from the Chad Basin in central Africa demonstrate that fossil hominid remains are not restricted to the eastern part of Africa. The success of exploration in paleoanthropology depends on the discovery of appropriate sediment layers, mainly lake and river deposits with an upper Miocene through Pleistocene age. Knowledge of the geological framework is of great importance in evaluating the potential for fossil preservation in a certain area. To date, three major types of geological megastructures have yielded almost

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O. Kullmer (✉)
Department of Paleoanthropology and Messel Research, Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany
e-mail: ottmar.kullmer@senckenberg.de

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all fossil remains of early hominids: the East African Rift Valley (EARV), the intracratonic basin of Lake Chad, and the fossil-rich cave deposits in South Africa. Each of these regions provides a unique sedimentary setting bearing fossil-rich layers comprising a specific time-span within the last few million years.

Introduction

The fossil record of humans is scanty, and discoveries are rare. It seems that the farther back in time we go, the fewer the fossil remains we can expect (Cooke 1983). There are probably several factors involved in diminishing the hard evidence of our own evolution. When a mammal dies in the open, scavengers will immediately work on the carcass, scatter its pieces, and probably destroy the bones (Shipman 1981). The surviving parts may be exposed to the hot sun during the daytime, and cooled down at night. Extreme temperature differences between day and night lead to cracking due to loss of water and reduction of organic material in the bone fibers. Usually, this process is accompanied by the activity of microorganisms, and may be also by physical transport in riverbeds or on floodplains during torrential rain falls. All of this modifies the original surface of bone, or even breaks elements apart. Most of the time, the history of an animal body ends in its complete destruction, unless the bones are covered and protected, e.g., by rapid burial with sediments (Cooke 1983). Sometimes animals are trapped in cavities, like fissures or pits, and their bones are preserved articulated. But even if we have a favorable environment for rapid covering, most of the time, postburial chemical and physical processes are destructive, with some rare exceptions favored by special geological environments.

For this reason, the search for hominid fossils depends at a larger scale on the geological setting, because the sedimentary environment is a limiting factor upon chances of finding early hominids. Due to the multifarious influences for destruction, each fossil we collect seems to be a stroke of luck. In Africa, the hunt for the discovery of the origin of mankind concentrates on three major types of geological settings with a great potential for new discoveries. These are graben structures (e.g., Chorowicz 2005), cave deposits (e.g., Brain 1981), and intracratonic basins (e.g., Vignaud et al. 2002) that developed during the last 8 million years (Ma), after the hominids diverged from their last common ancestor with the African great apes. Consequently, the East African Great Rift Valley (EARV), with its widespread outcrops of fossil-rich Miocene to Pleistocene deposits, presents a unique situation for paleoanthropological field research. The Rift provided permanent water sources for our oldest ancestors and a rich fauna (WoldeGabriel et al. 2001; Pickford and Senut 2001). A very similar situation is found in intracratonic basins like the Chad depression, occurring as relatively static systems with large lake transgression and regression cycles, varying in time, and sometimes producing fossiliferous deposits of enormous lateral extension (Vignaud et al. 2002). In contrast, the famous South African cave sites, Makapansgat, Sterkfontein, Swartkrans, and Kromdraai, were formed by extensive freshwater karstification and sedimentation processes, and their complex cavities were used as shelters for hominids and probably functioned also as traps and scavenger caves (Brain 1981).

Geological and paleoanthropological research at African hominid sites has produced a rich database during the last century (Bromage and Schrenk 1999). Today the geological background information influences the search for the origin of humankind, and the growing knowledge about geology helps us to understand the processes of fossilization and supports the interpretation of individual situations at fossil localities. And the application of digital geographical information systems (GIS), in combination with high-resolution satellite images, has provided a huge additional database for field investigations (e.g., Anemone et al. 2011). Potential fossil localities, in Rift valleys, intracratonic basins, and karstified limestone, can be localized by satellite image analysis. Nevertheless, extensive surveys by experienced field teams will continue to be the fundamental basis for the discovery of new fossil hominid remains (Fleagle and Gilbert 2008).

Geological Setting

The geological setting at hominid localities is not only an important source of information about environmental settings and changes through time in specific localities or areas, but also an indicator of the probability of finding fossilized bones; and it is therefore an essential aspect influencing survey strategies. Moreover, it is an important aspect of the transfer of knowledge relevant to a broad understanding of human evolution as a Pan-African story (Schrenk et al. 2004).

Sedimentary formations with a high potential for fossilization are the required geological setting. These consist of deposits that are products of weathering and transport, erosion, and deposition. Sediments are a mixture of different minerals and organic materials deposited on the earth’s surface, or in caves, in interaction with the atmosphere, hydrosphere, and biosphere. Common examples are clays, silts, sands, gravels, and breccias. Due to subsidence of some hundred meters, up to a few kilometers, deposits are typically transformed into sedimentary rock, like sandstone, claystone, or limestone.

Accumulation areas of sediments are divided into marine and continental depositional space.

Even if some of the fossil sites, like Saldanha or Klasies River Mouth in South Africa, are located closely to the ocean shoreline, the most important hominid fossil sites are located in continental deposits. Potential continental bone accumulation localities are fissures, caves, swamps, tar pits, river channels, flood plains, lagoons, and lakes. Such depositional areas can be described as geomorphological units characterized by climate, size, and shape of a sedimentary basin. Geometry and composition of sediments, and the relationship between units, provides information about the milieu of deposition (Reineck and Singh 1980). Physical, chemical, and biological parameters (Table 1) inform us about the depositional environment and climatic conditions. These parameters have to be recorded during fieldwork. The sum of all primary characteristics of a sedimentary unit defines the sedimentary

Table 1 Sedimentary parameters of depositional environments

Physical	Surface features (ripple marks, load casts, shrinking cracks, etc.)
	Depositional features (horizontal/cross bedding, grain size, etc.)
Chemical	Crystallization (carbonates, salts, etc.)
Biological	Biogenetic remains (bones, teeth, shells, phytoliths, etc.)
	Bioturbation
	Excrements (coproliths, pellets, etc.)
	Organic remains (plants, bacteria, etc.)
	Bioerosion (gnawing marks, burrows, etc.)
	Biostratification (stromatoliths, etc.)

After Reineck and Singh (1980)

Table 2 Sedimentary factors of depositional environments

Physical	Medium
	Current
	Wave intensity
	Velocity
	Water depth
Chemical	Mineral composition
	Groundwater composition
	Climate
Biological	Faunal remains
	Floral remains

After Reineck and Singh (1980)

facies (Reineck and Singh 1980). The analysis of the facies permits us to understand the sedimentary factors responsible for the appearance of the deposit and the fossils.

Medium, current, wave intensity and velocity, as well as water depth, are relevant physical factors (Table 2); these are the important hydrodynamic conditions for the transport of animal remains. Mineral and groundwater composition, including climate, are understood to be the chemical factors of sedimentation and fossilization. Fortunately, sediments sometimes contain biological factors, faunal and floral remains, in different stages of preservation. The appearance of animal remains in a sedimentary matrix depends on its so-called taphonomic history (Shipman 1981). The taphonomy (Efremov 1940) includes two processes, biostratinomy and diagenesis, that describe the pathway from a carcass to a fossil. Biostratinomy (Weigelt 1927) deals with everything that happens to a carcass after an animal's death, before the remains are buried. Afterward, the fossilization process, including mineral exchange and compaction, is called diagenesis. The fossilization process reduces information about an animal, but it also tells us a story that contains information about the paleoenvironment. The possibility that parts of a given animal will survive for some million years is relatively low due to taphonomic factors. Fossils are not randomly distributed. There are only a few spots on earth where we can find mammal remains, and there are even fewer places where we can discover hominid fossils. In most assemblages of large mammals from a single locality, the abundance of hominid specimens is less than 0.5 %.

Nevertheless, the number of collected fossils has increased rapidly during the last decades. More and more research teams, with sophisticated survey strategies, explore for and investigate new fossil sites (Urbanek et al. 2005; Kullmer et al. 2008). Extensive sedimentologic and taphonomic analyses at known localities lead to a broad understanding of fossil site creation (Bobé et al. 2007).

Commonly, the geographical distribution of hominid localities is used to interpret the origin of mankind and the migration patterns of early hominids (Coppens 1994). One has to consider, though, that the interpretation of the biogeography of a species, or even of an evolutionary lineage, can be heavily biased by the factors mentioned earlier, as well as by others such as burrowing and the preservation of animal remains (chapter "▶ Taphonomic and Diagenetic Processes," Vol. 1).

White (1988) pointed out that the fossil record in eastern Africa is biased toward a representation of the watered axial basins. Classic hinterland sites lacking permanent water sources, e.g., Laetoli, are rare indeed. But this does not imply that these were minor constituents; they may just have not been discovered yet. The preservation of fossils is heavily dependent on the sedimentological environment (e.g., WoldeGabriel et al. 2009). Fluviatile milieus do not necessarily grant permanent burial; many of the fossil localities in eastern Africa are associated with rivers, and a migrating channel bed can alter even a lake margin or a floodplain within a short time period.

Chances of finding an original bone association decrease with the transport distance from the point of origin. When discovered, the bone assemblage is likely to represent different individuals from different localities and different time periods (Hanson 1980). Time averaging, the mixing of noncontemporaneous populations, has also to be considered when interpreting the history of bone assemblages. Nevertheless, beside sedimentological factors, the effects of time averaging are also dependent on stable or highly fluctuating populations (Behrensmeyer and Chapman 1993).

East African Rift Valley

If we look at the geographical distribution of early hominid findings in Africa, we recognize that many of the famous sites are aligned in a chain along eastern Africa from Ethiopia via Kenya and Tanzania, to Malawi in the southeast. Localities like Hadar, Middle Awash, Omo, Lake Turkana, Olduvai, Laetoli, and others have yielded a great number of hominid specimens during the last 50 years (chapters "▶ The Species and Diversity of Australopiths," "▶ The Earliest Putative *Homo* Fossils," and "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). These sites are positioned in a geological megastructure, the EARV (Fig. 1). The EARV extends about 6,400 km from northeast to southeast.

The suture of the EARV follows a fault zone in the Continental crust. Plate tectonics explains the process of break-apart and rifting (Chorowicz 2005).

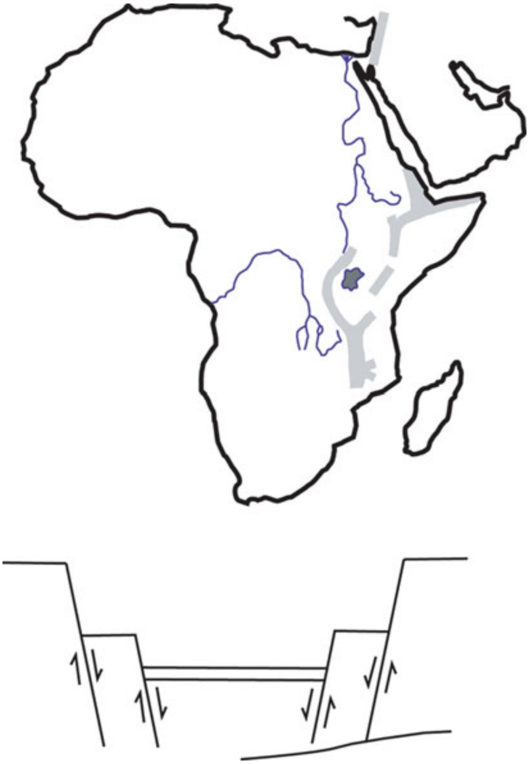

Fig. 1 The geological megagraben of the EARV (*gray area*) with its famous hominid sites extends over more than 6,400 km from the Gulf of Aden and the Red Sea in the north into the Indian Ocean in the southeast, at the level of Madagascar. The main rift splits into eastern and western branches just north of Lake Victoria. A schematic transverse section (*below*) through the Rift Valley shows that the graben shoulders are composed of a stepped block-system separated by normal faults. The center is lowered due to crustal extension and divergence and uplift of the shoulders

The Nubian and Somalian plates diverge along the main rift axes and result in a great graben with an average width of 30–40 km. The flanks are uplifted, while subsidence forms the graben floor. Active east–west extension leads to an enlargement of the accumulation space. A sedimentary fault basin develops as soon as the subsidence is great enough that an initial drainage system grows along the main faults. Minor rivers and alluvial fans transport material into the basin from the rift shoulders. A complex erosion-sedimentation interaction system starts in the active rift zone.

The expression "rift," or "rift valley," can be traced back to the definition of Gregory (Gregory 1896). Accordingly, a rift valley, like the Malawi Rift, is a parallel-sided down-faulted valley some tens of kilometers in width and at least a few hundred kilometers in length (Ring and Betzler 1995). Several smaller-scaled tectonic structures, like halfgrabens, horsts, warped blocks, major faults, transform faults, and pull-apart basins can occur within a rift system. All these geological structures provide space for accumulation, and for erosional processes to bury and unearth skeletal remains.

In the history of a mature rift system, diverse environmental settings may be recorded, representing a wide range of habitats (chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1). Rifting may end in a marine transgression phase and the birth of an ocean, when the continental breakup continues and rift floor subsidence extends toward the coast, as we can observe happening in the Red Sea and the Gulf of Aden. In other cases, the rifting dynamics may stop after some active phases.

The EARV is probably one of the most attractive and interesting rift systems, reflecting several stages of rift development in its longitudinal extension. It therefore provides an important field of research for understanding crust breakup in a continental setting. Over the last 110 years, extensive research has been focused on the EARV (Gregory 1896; Wegener 1912; Krenkel 1922), making the East African rift system one of the best documented continental rift systems on Earth (Ring and Betzler 1995). Two areas have been of major interest: the Ethiopian Afar Triangle (Baker et al. 1972; Mohr 1987) in the Northeast at the horn of Africa, because of its special rifting situation as a triple junction of three crustal plates (Beyene and Abdelsalam 2005); and the Kenyan or Gregory Rift (Baker et al. 1972, 1988; King 1978; Crossley 1979; Strecker et al. 1990), as the eastern branch of the graben system.

Extensive magmatism and volcanism has accompanied sedimentation in the graben. The oldest rifting phases are recognized in the northeastern part, at the western boundary of the Sinai Peninsula marking the boundary of the Arabian plate. The Red Sea and the Gulf of Aden are probably the oldest segments of the rift system, starting with its initial uplifts and doming of the crust, probably in the Oligocene. Initial volcanism is evident as early as the Eocene (e.g., Trap series), producing widespread lava (Beyene and Abdelsalam 2005). In the Miocene, thick flood basalts produced by large shield volcanoes filled the proto-rift in the Afar region. A highly active rifting phase followed in the Miocene, and produced accumulation space for extensive sedimentation of the erosional material from the rift shoulders and the rift volcanism. Sedimentation was always interrupted or accompanied by flood basalts and other volcanic eruptions, changing the landscape and sedimentation environments within the basins.

There is no doubt that due to the spreading process, the EARV witnessed some habitat changes in eastern Africa. Faulting, uplifts, and subsidence support the development of all common fluvial processes, with meandering and braided rivers, flood plains, alluvial fans, oxbow lakes, and natural levees. Major rift lakes, like Lake Turkana, developed permanent water sources during long-term transgression phases. Regression/transgression cycles are evident through changes in sedimentary formations (Frostick et al. 1986).

Afar Depression

The Afar Depression in Ethiopia (Fig. 2) is one of the world's hotspots in two ways. The temperature can climb up to more than 45 °C during daytime in the endless plains of the Afar, and fieldwork is a great challenge in the extreme African sun. Still, for paleoanthropologists and paleontologists who deal with the evolution of early humans, this investigation can be of the greatest interest since the area of

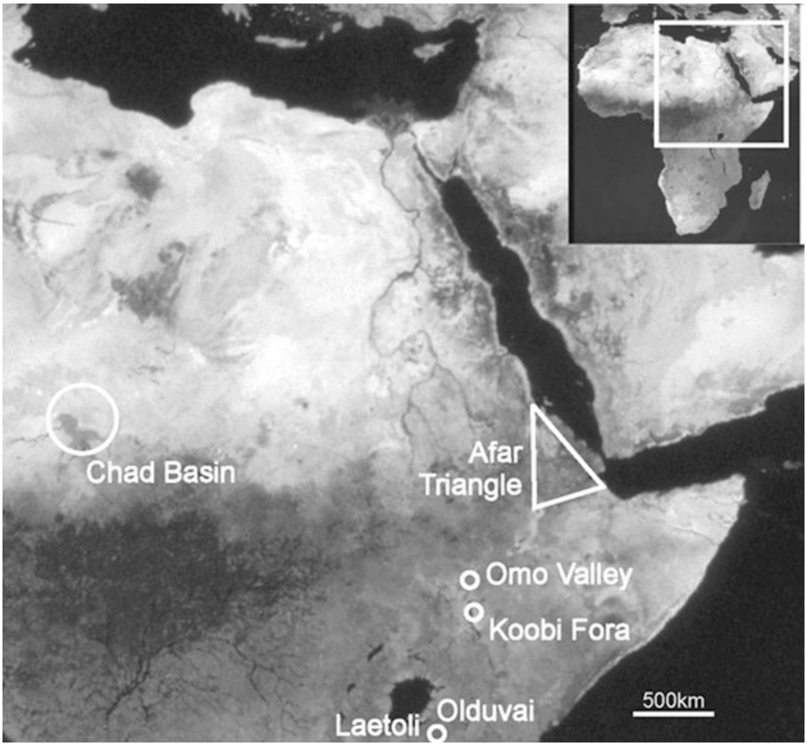

Fig. 2 The outlines of the Afar depression in the northeast of Ethiopia draw a triangle of about 150,000 km^2. This huge basin contains fossiliferous sediments ranging in age from the Upper Miocene to recent times. The most famous hominid localities in the Afar triangle are at Hadar and in the Middle Awash. The Omo Valley is located far south in the main rift, where the Omo river crosses the border into Kenya. The fossil-rich area of Koobi Fora belongs to the Lake Turkana localities in Kenya, where thick sediment deposits surround the recent Lake. Olduvai and Laetoli are positioned within the eastern branch of the EARV, while the Chad Basin reflects an intracratonic depression about 2,500 km west of the Great Rift Valley with widespread deposits of the ancestral Lake Chad

about 150,000 km^2 bears some of the richest hominid sites in the world. In that context, the Afar Depression contains fossils from the earliest time interval of humankind, 5–6 Ma, right up to the youngest (WoldeGabriel et al. 2001, 2009).

Since the beginning of the 1970s, the Afar Triangle has been in the spotlight of international paleoanthropological field research. Numerous hominid findings, like the skeleton of the famous “Lucy,” come from here (Taieb et al. 1974,) (chapter “▶ The Species and Diversity of Australopiths,” Vol. 3). Paleontological work in Ethiopia started in 1902, when the Frenchman Robert de Bourg de Bozas discovered fossil-rich deposits in the lower Omo Valley north of the Kenyan boundary (Fig. 2).

Nevertheless, the first fossil hominid from Ethiopia, a lower jaw, was discovered only in 1933, in a cave close to Dire Dawa in the east. Likewise in 1933, the French paleontologist Camille Arambourg led an expedition to the fossiliferous sediments of the Omo River (Arambourg 1933). Although no hominid remains were discovered during the field trip, the team collected numerous animal fossils (Arambourg 1947). In 1967, an Ethiopian-American-French-Kenyan team under the direction of Clark Howell and Yves Coppens, and with the collaboration of Camille Arambourg, started the intensive search for hominid fossils in the Omo region (Arambourg et al. 1967; Arambourg and Coppens 1968a, b; Coppens et al. 1976). By 1973 they had recovered several hominid remains in the Usno, Mursi, and Shungura formations in the Omo River Basin. This initiated a "hominid-rush" in Ethiopia, which continues today.

When the French geologist Maurice Taieb in 1970 announced the discovery of fossil-rich deposits at Hadar, further north in the Afar depression, the search for hominid remains shifted into the Afar region (Taieb et al. 1972, 1974). It was at Hadar that Donald Johanson and his team found the most complete *A. afarensis* skeleton in 1973 (Johanson et al. 1978). Inspired by a Beatles song, they named it "Lucy" (Johanson and Edey 1981). From 1975 to 1978, the American geologist Jon Kalb explored, with his colleagues of the "Addis Abeba Rift Valley Research Mission in Ethiopia" (RVRME), the sediments in the "Middle Awash" region (Kalb et al. 1982a, b), where they documented one of the best known lithological sequences in the Afar Triangle containing fossil evidence of human evolution. The sediments cover a time-span of more than 6 Myr. Intercalated volcanic ash and lava horizons permit the absolute dating of sandwiched river and lake deposits, and thereby provide a unique insight into the evolutionary history of humankind. Since the early 1990s, Tim White and his "Middle Awash Research Project" have investigated these deposits successfully, collecting a large mammal assemblage including numerous hominid fossils such as the first remains of *Ardipithecus ramidus* (chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3) (White et al. 1994). Since the of 2000, the international PAR-Team (Paleoanthropological Research Team), under the direction of Horst Seidler, has investigated deposits further south of the "Middle Awash" in a fossil-rich area in the Somali region called Galili (Weber et al. 2001), about 100 km north of the Awash railway station and town, in the vicinity of the rift shoulder (Macchiarelli et al. 2004; Urbanek et al. 2005; Kullmer et al. 2008).

Central Rift

Further South in the EARV, in the Turkana Basin of northern Kenya, Richard Leakey and his team started to explore the eastern shore of Lake Turkana from 1968 through the early 1970s (Leakey and Leakey 1978), while investigations in the Omo River Valley were continuing. They surveyed the areas in the vicinity of Koobi Fora (Fig. 2), a place where fossil bones were reported as early as 1940, and mentioned by the District Commissioner of Marsabit to Dr. L.S.B. Leakey, Richard Leakey's father (Leakey 1978). The Koobi Fora Research Project collected fossils including many hominid remains from Plio-Pleistocene lake, river and flood plain silt, and sand deposits that are bordered by Miocene volcanic lava in the east and south, and by the recent Lake Turkana in the west.

Extensive volcanic activity accompanied the rifting process along the major axis of the rift valley, forming depositional bodies with material from ash rains and lava flows. Those tuffs, basalts, and ignimbrites are important marker horizons, intercalated in the sediment successions. Radiometric dating allows the determination of their absolute age, and therefore also of the sandwiched fossil-bearing sediments at many hominid sites, in a region running from north of Lake Turkana in the Omo Valley, along the eastern and western shoreline, and into the southwest at Kanapoi and Lothagam. The sediment succession tells a story of transgression and regression phases during the development of the great graben (Trauth et al. 2005). Today, sediments of different age outcrop at the same level alongside them, due to small-scale tectonics producing uplift and subsidence of single blocks and leading to a patchwork of sedimentary deposits. To sort the sediments into a logical lithostratigraphic column at a particular fossil locality is one of the many challenges for sedimentologists reconstructing the sedimentary settings. It took many years to reconstruct the development of the sedimentary bodies deposited during the last 6 Myr at Lake Turkana.

Further south in the EARV, the axis of the major graben seems to be nebulous. On a larger scale, the continental fracture in the earth's crust splits in northern Tanzania into western and eastern branches, forming a large island structure between them that holds an intracratonic basin, a large depression with Lake Victoria at its center. The western branch of the EARV, with its northern deposits at Lake Albert in Uganda, has also produced a rich fauna, eroding from lake beds and river deposits from the Upper Miocene onward (Pickford et al. 1993).

So far no hominid fossils have been discovered in these sediments, whereas in the southern part of the eastern branch, the fossil localities of the famous Olduvai Gorge in northern Tanzania have produced many hominid remains. In the vicinity of Olduvai, a remarkable magmatic province, with the Ngorongoro caldera, Lemagrut, Sadiman, and Oldeani volcanoes, produced immense amounts of ash during Plio-Pleistocene times, including the thick volcanics that mark the base of the Olduvai succession. The volcanic eruptions supported the creation of a fossil site that seems to be unique in the EARV. Most likely the oldest volcano, Sadiman (K-Ar age of 3.7 Ma), was the source of the volcanic sediments of the Laetoli region (Hay 1987). The distinctive geochemical composition is compatible with the Laetolil Beds, while Lemagrut and Ngorongoro produced lavas of a different petrology. The fossiliferous Laetolil Beds, close to the village Endulen, were discovered by some local Masai. Erosional processes unearthed several hominid remains, and in addition, a rich fauna was discovered. The first hominid remains at Laetoli were collected by a German explorer, Kohl-Larsen in 1939, 4 years after the first visit to Laetoli of Mary Leakey. She traveled again to Laetoli in 1959 (Leakey 1987), while she and her husband Louis were excavating in the sediments of the famous Olduvai Gorge in the North. Later in the 1970s, Mary Leakey discovered one of the most remarkable pieces of evidence for the upright gait of early hominids: a footprint trail in a volcanic ash deposit. The lowermost sediments, the Laetolil Beds, were deposited on an uplifted peneplain prior to movement along the Eyasi Fault (Hay 1987), a large fault creating the steep Lake Eyasi cliff. Some modern inselbergs give evidence of the uneven surface of the peneplain, where the sedimentary deposits in the valleys mark the paleodrainage and point to east–west as the major flowing direction. Obviously, the steep Eyasi fault did not exist when the water-laid deposits developed (Hay 1981), because today the river systems in the south flow more or less perpendicular to the Eyasi fault. The Laetolil Beds deposits are divided into dominantly water-laid tuffs in the south, with the addition of extensive aeolian tuffs in the north. In the upper sequence, some lava flows and clay deposits occur. In recent times, doming and resulting uplift led to erosion in the Laetoli region and to the exposure of the stratigraphic sequence of fossil-rich sediments (Ditchfield and Harrison 2011).

Chad Basin

While today water erosion and fluviatile deposition during short and heavy rainy seasons is the most active land-forming process in the eastern African savanna, the Sahara desert is dominated by wind erosion and dune deposition. Brunet et al. (1995) reported the first *Australopithecus* remains far west of the EARV from the desert of central Africa, more than 30 years after Coppens (1961) announced the first hominid discovery in Chad. Since 1994, the Mission Paléoanthropologique Franco-Tchadienne, led by Michel Brunet, has explored Miocene and Pliocene deposits in the Djurab Desert of northern Chad. The deposits are located in a large intracratonic basin, which includes modern Lake Chad in the southern sub-basin, and the Chad lowlands in the northern sub-basin (Vignaud et al. 2002). Fossiliferous sediments in the basin have been known since 1960, when Coppens reported Quaternary fossils from Koro Toro (Coppens 1960).

Recent aeolian deflation in the northern sub-basin formed the Djurab Desert, with arid conditions, while the southern depression, under semiarid to wet conditions, reflects the latest lacustrine episode in the region. A "Mega Lake Chad" existed in Holocene times, but progressive desert extension of the Sahara toward the south reduced the water column of Lake Chad to its present shallow-water situation. An average water depth of 2–4 m can be measured today, and compares with a maximum depth of 180 m during ancient times. The basement of the Chad Basin is built of Precambrian rock, and forms a large depression which is filled with lacustrine, fluviatile, and lake sediments. The fluviatile facies is described by flooding channels, probably deposited during torrential rainfalls, because no mature river system, like meandering or braided channels, is reported (Vignaud et al. 2002).

In the northern sub-basin, extensive aeolian sands contain well-sorted quartz grains, frequently formed since Upper Miocene times as dunes and shifting sands. The fossil content, including rich fish remains, crocodiles, and semiaquatic mammals like hippos, gives evidence of a permanent water source during the time when *Sahelanthropus tchadensis* (chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3), the oldest known hominid, lived probably in a gallery forest along the shoreline of Proto-Lake Chad. The so-called anthracotheriid unit of the *Sahelanthropus* site is interpreted to be a shallow perilacustrine environment, and consists of a well-sorted and well-cemented sandstone. It yielded all the terrestrial vertebrate remains (Vignaud et al. 2002).

However, the desert already existed in the vicinity, and produced sedimentary material through aeolian deflation that gradually covered the lake floor and also animal carcasses. Along the flat margin of the ancient lakes, drainage systems developed during rainy seasons. Floods reworked the aeolian deposits surrounding the lake. Temporarily thin soil layers developed on floodplains, as confirmed by root casts developed in the major fossil layer at the *Sahelanthropus* locality Toros Menalla (Vignaud et al. 2002). The sedimentary situation in the Lake Chad Basin is controlled by transgression and regression phases of the lake and the Sahara desert (Schuster et al. 2006).

South African Caves

In South Africa, the famous hominid sites of Sterkfontein, Swartkrans, Kromdraai, and Makapansgat (Fig. 3) are formed in a very specific geological setting that contrasts with the eastern African hominid localities. The fossil hominid-containing sediments accumulated in caves developed in Precambrian dolomite limestones, in Plio-Pleistocene times, through extensive karstification. The cave limestones belong to the Malmani Dolomite, which is part of the Transvaal Supergroup (Eriksson et al. 1976). The age of the Malmani dolostones, deposited in the intracratonic Transvaal Basin, is considered to be between 2.5 and 2.6 billion years (Button 1973). The thickness of the deposits reaches 1,450 m in the Sterkfontein area (Eriksson and Truswell 1974), and there is a large sedimentary hiatus from the Precambrian to the Late Tertiary. Abundant faulting and folding of the dolomite limestone makes determining the exact stratigraphic position of the basic cave material difficult. The occurrence of stromatoliths in the Makapan Valley led to the idea that at least some of the limestone sediments had been formed in the intertidal zone (Eriksson et al. 1976) near the shore line of the ancient sea.

The initial cave development probably followed the fracture pattern in the dolomite rock, and extensive and deep karstification took place due to groundwater level changes. A typical feature of the Transvaal karst is the occurrence of a three-dimensional hyperphreatic maze of fissure passages (Martini et al. 2003), although large caverns did develop. As a result of erosion, cave ceilings collapsed and opened larger chambers. Carbonate solutions and mineralization built up thick travertine layers on the floors. The rich travertine deposits attracted miners at the end of the nineteenth century because of their pure calcium carbonate content. On the other hand, the carbonate is responsible for the consolidation of clastic sediments that filled up caverns through openings from the land surface. Sand, chert, dolomite, quartzite materials, and also bones were washed down into the caves. Winds probably brought fine grains, following the law of gravity. Possibly several

Fig. 3 The caves at Makapansgat belong to a large Precambrian dolomite formation (*above*), showing profound karstification and sedimentation during Plio-Pleistocene times. Limestone cavities (*below*) are filled with travertine and characteristic carbonatic bone breccias. Mining for carbonates hollowed the filled cavities and brought thousands of fossils to light. The preservation of the fossils differs from sites in the EARV due to very different processes of site formation

transporting agents led to the high bone accumulation at some localities in the cave systems. Some of the caverns were completely filled up with exogenous material, and their sediments concreted to cave breccias with a fine-grained matrix and carbonate cement. Differences in color and grain size may indicate different modes and phases of sedimentation. Accessing the bones, which are enclosed in the breccias, demands sophisticated physical and chemical preparation techniques.

Gravity and water transport, together with typical processes like collapses, solution, and remineralization, are responsible for the complex geological setting of many of the caves. The extensive lime works in the South African caves brought thousands of bone fragments to light, although blasting operations destroyed many natural features of the caves. Consequently, reconstruction of the diagenesis of the South African cave sites has been a real challenge, and many aspects still need further investigation. The analysis of the taphonomic history of bone accumulations at the South African cave sites needs detailed on-site observations, and also further lab work. Bob Brain and his team investigated many years at Swartkrans before he came up with his last model of cave development, in which he proposed nine diagenetic steps (Brain 1993). The formation started with a probably Miocene cavern below the level of standing water. After the opening of the cave, surface sediment began to accumulate inside the cave. The interpretation of the fossiliferous “pink breccia” of the Outer Cave, which was shown to be an infilled remnant, the Hanging Remnant Unit of Member 1, proved to be especially time-consuming.

Swartkrans Members 1–3 yielded *inter alia* the remains of *Australopithecus robustus*, which is likely to have an age of 1.8–1 Ma. Members 4–5 are Middle Stone Age and ca. 11,000-year-old, respectively.

Extensive investigations at Swartkrans and other South African cave sites have led to definitive models of the development of the deposits, and their fossil content in time and space. The experience and strategies used in the past provide the knowledge, which together with modern dating methods (Pickering et al. 2007) allow further exploration of development of fossil sites in the karstified limestones in South Africa.

Conclusions

Although it seems to be clear that the chance of finding hominid fossils is limited by the factors mentioned earlier, there is no doubt that many fossils still await unearthing, either by erosion or by humans. The types of sediments and the geological contexts likely to yield hominid fossils are known. We just have to look for the right deposits. So far, early hominids have only been discovered in eastern and southern Africa, with the exception of the Chad Basin in central Africa. This is probably due to the auspicious geological setting and time represented in the EARV, rather than reflecting the paleobiogeographic distribution pattern of early hominids, although the occurrence of permanent freshwater sources, represented, e.g., by large rift lakes, probably attracted early hominids, because they were not capable of carrying a larger amount of water from one location to another.

No doubt the hominid richness of the Rift sediments is unique altogether. There is still a high potential to recover more remains at long-known places, because erosion is always at work, and the immense deposits in the EARV are far from fully explored. Huge areas, for instance, in the Afar Triangle and in other places, have never been surveyed for fossils. New techniques, like satellite imagery with a resolution of a few meters on the ground, are of potential help for exploration work. Additionally, airborne survey can provide access to remote places such as the Danakil depression in the northern Afar. Nevertheless, extensive studies of satellite images will almost certainly discover new fossiliferous localities in smaller-scaled graben and basin structures at places in central, western, or southwestern Africa. It seems just a matter of time until the first early hominid is reported from the other side of the African continent.

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Paleosols

Gregory Retallack

Contents

Abstract

Soils are known to be products of environmental factors such as climate, vegetation, topographic setting, parent material, and time for formation, so that paleosols, or fossil soils, can potentially reveal changing environments of the past. Evidence from paleosols for past climate and vegetation in East Africa does not support traditional narratives of human evolution during a single transition from primeval forest to dry climate and open grassland. Instead, paleosols indicate climatic oscillations between wet and dry, and alternating expansion of woodland and grassland, since at least 18 Ma (million years ago). Acquisition of dry grassland adaptations such as thick enamel by 18 Ma, adducted hallux by 14 Ma, and cursorial legs by 1.8 Ma, alternated with woodland adaptations such as short stiff back by 16 Ma, erect stance by 6 Ma, and flat face by 3.5 Ma. Our ancestors survived profoundly changing climate and vegetation, with some adaptations lasting only to the next environmental shift, but others proving to be of lasting value.

G. Retallack (✉)
Department of Geological Sciences, University of Oregon, Eugene, OR, USA
e-mail: gregr@uoregon.edu; gregr@darkwing.uoregon.edu

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Introduction

Our species, and its ancestors of millions of years ago, evolved on the soils of Africa (Darwin 1872; Fleagle 1998). Many of those soils have been eroded or altered beyond recognition by deep burial, but many paleosols are buried within floodplain, volcanic, lacustrine, alluvial plain, and cave deposits of Africa (Retallack 2001a). These paleosols provide much of the colorful banding and mottling seen in East African badlands and dongas, including many fossil hominoid localities (Fig. 1). Many fossils of human ancestors come from paleosols (Retallack et al. 1995, 2002; Radosevich et al. 1992; Wynn 2004a, b), which are also records of past environments of our evolutionary antecedents (Fig. 1). Modern soils are known to be products of environmental factors such as climate, vegetation, parent materials, topographic setting, and time for formation (Jenny 1941). These formative factors can be interpreted from fossiliferous paleosols to provide hitherto unavailable details of the habitats of fossil apes and humans.

The vegetation of fossil ape and human sites is central to long-standing theories of the evolution of upright stance. “The hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, ‘. . . so long as they were especially fitted to climbing trees’” (Darwin 1872). Other ideas are that grasslands selected for upright stance because of the need to be vigilant against predators (Dart 1926), to manipulate small seeds (Jolly 1970), to minimize exposure to the sun (Wheeler 1984), or to cover long distances with less energy by walking (Rodman and McHenry 1980) or running (Bramble and Lieberman 2004). Wooded grasslands and open woodlands are also plausible sites for evolution of upright stance from squat feeding on the ground (Kingdon 2003) or moving between scattered fruiting bushes (Sanford 2003). Alternatively, upright stance may have evolved in forests because it allowed erect-back climbing (Tuttle 1981), hands free to care for premature infants (Lovejoy 1981), phallic display to females (Tanner 1981), or intimidation displays to rivals (Jablonski and Chaplin 1993).

Paleosols are relevant to these questions, because the fine root traces and crumb structure of grassland soils are distinct from the thick clayey subsurface horizons of both woodland and forest soils (Jenny 1941). Woodland and forest soils differ markedly in their clay minerals and chemical composition (Retallack 1997). Even the aquatic theory of human origins (Morgan 1982) can be evaluated from paleosols because mangal, littoral, lake margin, and streamside paleosols are distinguished by virtue of relict bedding and common burrows of crabs and clams (Retallack 2001a).

Paleoclimate also is of interest as a selective pressure on hominoid evolution through drought and other hardships. Paleoclimate was also a primary control of past vegetation in which hominoids found food and shelter. Paleoclimatic shifts to drier climate and more open grassy vegetation have been held responsible for major evolutionary innovations in hominoids and bovids (Vrba 1999), as have changes in degree of climatic variability (Potts 1996). Soils of dry climate have calcareous nodules at a shallower depth than soils of humid climate (Retallack 2005) and also

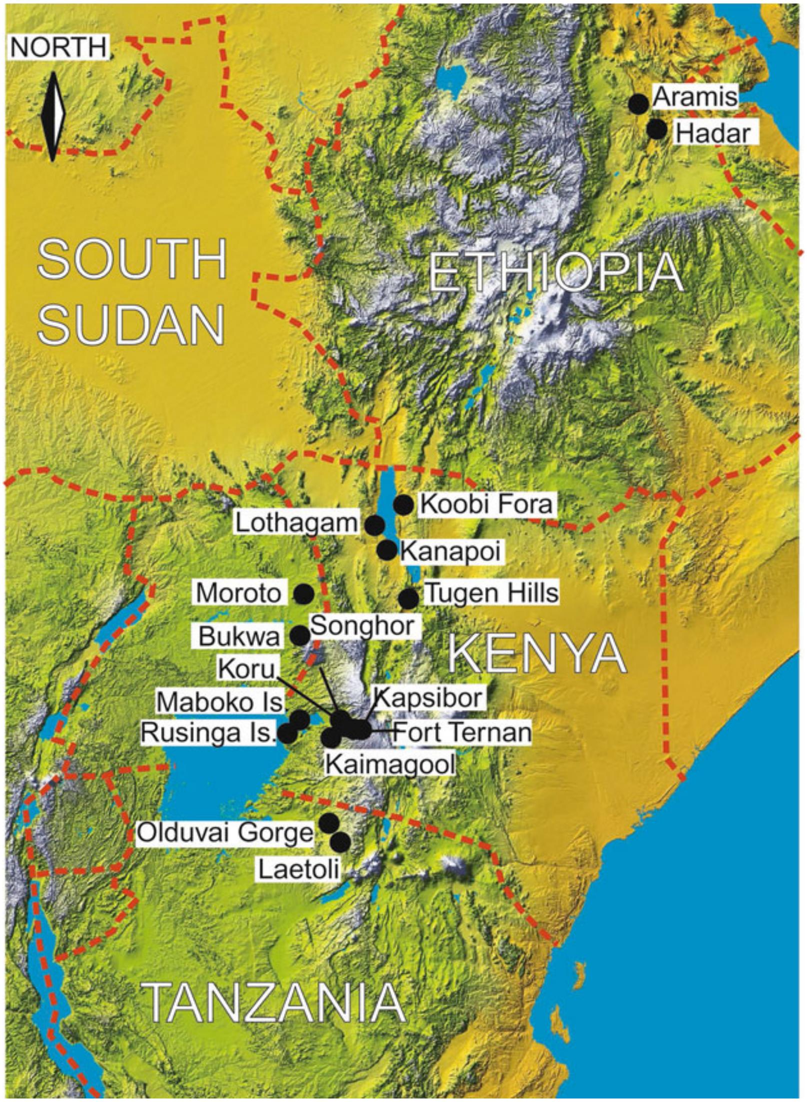

Fig. 1 Localities for paleosol studies in East Africa

are less leached of cationic nutrients (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}) than humid-climate soils (Sheldon et al. 2002). Paleosols can thus provide paleoclimatic records at the very sites of early human ancestors, rather than inferred from remote records of deep-sea cores (de Menocal 2004).

This review emphasizes climate and vegetation, but other soil-forming factors of parent material, topographic position, and duration of soil formation can also be inferred from paleosols. Highly calcareous and saline carbonatite volcanics are an unusual parent material of many African hominid sites (Retallack 1991a), fortunate because of their remarkable preservative effects for fossil bones, seeds, and insects (Retallack et al. 1995). Many East African paleosols preserve a record of well-drained fluvial terraces, infrequently flooded, and some volcanic apron paleosols represent foothills environments (Retallack 1991a), thus revealing environments beyond the usual lowland constraints of sedimentary environments. Degree of soil development can also be used to infer duration of paleosol formation and rates of sediment accumulation, with implications for the geochronology of ape and human ancestor sites (Retallack et al. 1995, 2002).

Recognition of Paleosols

Paleosols are often distinctive and striking bands of red clay (Bt horizon), calcareous nodules (Bk horizon), or coal (O horizon) in sedimentary and volcanic sequences (Fig. 2). Three general classes of observations are especially helpful in paleosol recognition: root traces, soil horizons, and soil texture (Retallack 1997).

Root traces are the most diagnostic evidence of paleosols, and fossil roots may be made more obvious by erosion-resistant cementation (Kabisa pedotype of Fig. 2). Difficulties arise in recognition of root traces, because they are often replaced by other minerals and ramify in three dimensions in such a way that one rock face reveals little of the overall pattern. Few fossil roots are carbonaceous or reveal histological structures like permineralized fossil wood (Retallack 1997). The original root has commonly rotted out, and the hole it occupied is filled with claystone or siltstone, or encrusted with iron oxide or calcium carbonate. Drab haloed root traces are very distinct, green gray mottles, in reddish paleosol matrix, formed during early burial chemical reduction by microbes fueled by consumption of root organic matter (Retallack 1991b). In all these cases, root traces are truncated at the surface of the paleosol, and branch and taper downward. These features distinguish root traces from most kinds of burrows in soils, although the relationship between burrows and roots can be complex. Roots may preferentially follow soft fill of burrows rather than hard soil matrix, and burrows may congregate around roots on which the burrowing animals fed (Retallack 1991a).

Soil horizons develop through thousands of years, whereas sedimentary beds are deposited in days. Unlike sedimentary beds, which have sharp bottoms and usually sharp tops as well, paleosols have a sharp top, representing the ancient land surface, but gradational lower contacts (Retallack 2001a). Sedimentary beds also include a variety of sedimentary structures, such as lamination, cross bedding, and ripple marks (as in Tek pedotype of Fig. 2), whereas soil horizons develop with obliteration of these original features (Tut pedotype of Fig. 2). Similarly, soil formation progressively destroys the original crystalline structure of volcanic or granitic parent materials (Retallack 1991a). In dry climate soils (Aridisols), primary sedimentary or volcanic structures are obscured at first by filaments and soft, small

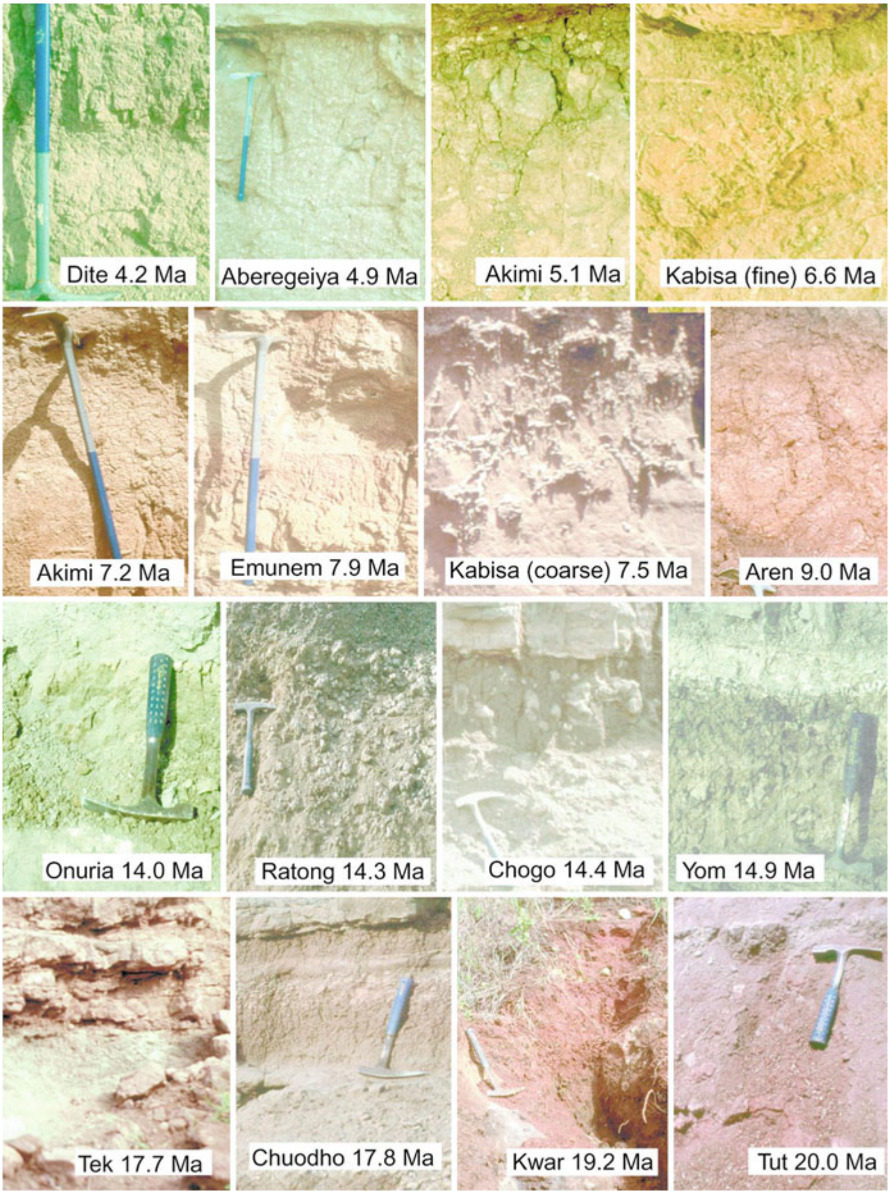

Fig. 2 Kenyan Miocene paleosols have been given field names using local Luo and Turkana languages. These pedotypes are objective field mapping units for paleosols: their interpretation and classification requires laboratory study

carbonate masses, then large, hard, carbonate nodules (calcic or Bk horizon of Chogo pedotype in Fig. 2), and finally thick carbonate layers (petrocalcic or K horizon of Soil Survey Staff 2000). In sod-grassland soils (Mollisols), primary lamination and crystalline structure is broken up by fine roots and replaced by dark, fecal pellets of earthworms to create a crumb-textured, organic surface horizon (mollic epipedon of Dite, Chogo, Yom, and Onuria pedotypes of Fig. 2). A variety of other kinds of soil horizons are recognized and important to soil classification (Retallack 1997, 2001a; Soil Survey Staff 2000).

Soil structure also develops within soil horizons, and is very distinct from sedimentary bedding and igneous crystalline texture. The fundamental elements of soil structure are modified cracks and other surfaces (cutans), and the clods they define (peds). Cutans include clay skins (argillans) lining cracks in the soil and rusty weathering rinds (sesquans) around clods and pebbles in soil (Retallack 2001a). Peds have a variety of shapes: lenticular in swelling-clay soils (Vertisols: Aberegaiya pedotype of Fig. 2), blocky subangular in fertile forest soils (Alfisols: Tut pedotype of Fig. 2), and crumb shaped (small and ellipsoidal) in grassland soils (Mollisols: Dite, Chogo, Yom, and Onuria pedotypes of Fig. 2). Although cracks and other voids are not preserved in paleosols due to compaction by overburden, peds and cutans are common and conspicuous (Retallack 1991a). Other soil structures less diagnostic of soils include concretions, nodules, and crystals (Retallack 2001a).

Methods for the Study of Paleosols

Just as soil individuals (pedons) are studied as soil columns in soil pits, paleosols are studied in columnar stratigraphic sections of the sort also used in sedimentology and stratigraphy (Fig. 3). Grain size is emphasized, because it is important to soil formation, as weathering transforms sand and silt grains to clay. A graphical representation of grain size profiles conveys important information on the abruptness of horizon transitions. Color from a Munsell chart should also be represented, as redness denotes the degree of chemical oxidation and drainage of soils and paleosols. Calcareousness determined by relative effervescence with dilute hydrochloric acid also is important as a guide to chemical leaching and soil nutrient status (Retallack 1997).

Laboratory studies of paleosols do not employ techniques identical to those used in soil science because some important soil measures, such as base saturation, are altered upon burial of soils (Retallack 1991b). Petrographic thin sections are especially useful for revealing soil microfabrics, and the point counting of thin sections furnishes estimates of changes in grain size and mineral composition of paleosols. For example, increased subsurface clayeyness can be used to recognize diagnostic horizons (argillic horizon) for forest soils (Alfisols and Ultisols), whereas traces of nutrient-rich minerals, such as calcite and feldspar, distinguish fertile forest soils (Alfisols) from infertile forest soils (Ultisols: Retallack 1997).

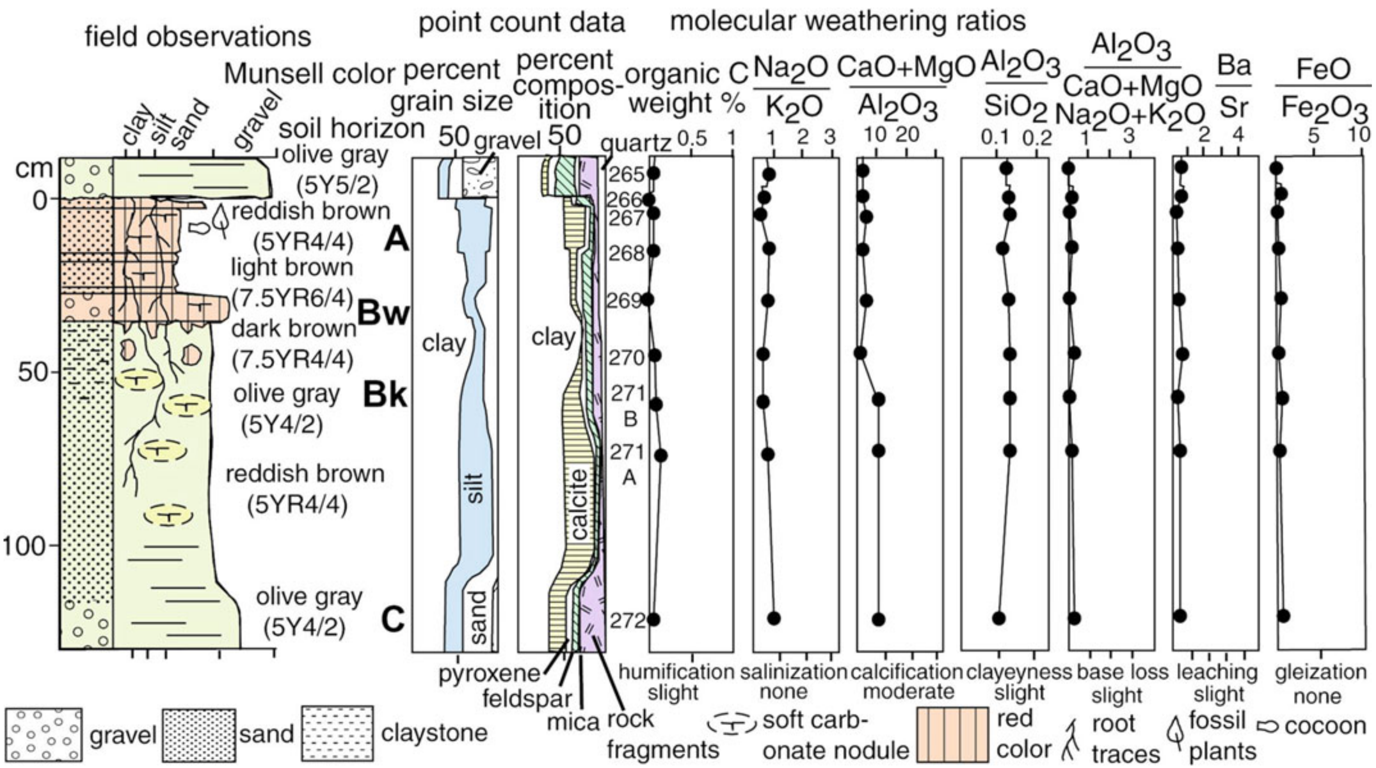

Fig. 3 Petrographic and chemical data for the Tek paleosol from the 18 Ma Hiwegi Formation of Rusinga Island, Kenya [Data from Retallack et al. (1995)]

Chemical analyses also are useful in characterizing and classifying paleosols, especially molar ratios designed to gage the progress of common soil-forming chemical reactions. The hydrolysis reaction common in silicate weathering leaches cationic bases (Ca^{2+}, Mg^{2+}, K^+, Na^+) from host minerals, such as feldspar, to create clay (Al rich) and is thus indicated by high ratios of alumina/bases. An alumina/ base ratio higher than 2 is a good proxy for the transition from fertile forest soils (Alfisols) to infertile forest soils (Ultisols). Soda/potash molar ratios in excess of 1 indicate unusually salty soils. Ferrous/ferric molar ratios in excess of 1 indicate well-drained soils (Retallack 1997). By these criteria, the petrographic and chemical data on the 18 Ma Tek paleosol from Rusinga Island Kenya (Fig. 3) indicate a fertile Inceptisol that was nonsaline and well-drained. These data allow identification of analogous modern soils (Retallack et al. 1995) and refine understanding of the ancient landscape and its ecosystem (Fig. 4).

Carbon isotopic compositions of paleosol carbonate were at first thought to be useful indicators of grasslands, because most tropical grasses have a C_4 photosynthetic pathway which creates isotopically heavy carbon (Cerling 1992). The most prominent failure of this technique was in its application to the Middle Miocene (13.7 Ma) locality of Fort Ternan (Pickford et al. 2006), with paleosol carbonate isotopically like rain forest (Cerling et al. 1997a), but fossil soils, grasses, trees, and antelope like those of a mosaic of wooded grassland and grassy woodland (Retallack 1991a, 1992; Koch 1998; Turner and Antón 2004). Subsequently, it was found that even tropical grasses used the C_3 photosynthetic pathway until about 7 Ma or younger (Cerling et al. 1997b; Fox and Koch 2003). The quality of graze (C_3 more nutritious than C_4) can be assessed by isotopic studies of teeth and paleosols, but the question of grass or shrub diet is better assessed from mammalian tooth microwear, hypsodonty, and cursoriality (MacFadden 2000). The advent of C_4 grasses within tropical grasslands is most likely related to declining Late Miocene atmospheric CO_2 content (Cerling et al. 1997a). Another failure of carbon isotopes to indicate past vegetation is Sike's (1994) forest interpretation of the paleosol at Olduvai fossil locality FLK yielding *Australopithecus boisei*. This paleosol, with relict bedding, zeolites, little clay, and shallow carbonate, is unlike forest soils, and probably supported salt-tolerant, lake-margin shrubs (Retallack 2001a), which have a similar C_3 isotopic value to forest (Sikes 1994). Isotopic values of carbon and oxygen in paleosols and animals are controlled by so many factors that biotic and pedogenic constraints are needed (Koch 1998). Carbon isotopic studies of paleosols are now more useful for assessing atmospheric CO_2 from carbonate and organic isotopic offsets (Ekart et al. 1999) and soil productivity from isotopic depth functions (Yapp and Poths 1994). Carbon isotopic depth profiles of paleosols also provide new insights into carbon cycling within different kinds of ancient ecosystems. Grassland paleosols (Chogo and Onuria pedotype of Fig. 5) show more effective humification at the surface (higher $\delta^{13}C$ values) than woodland soils (Tut of Fig .5), and swelling-clay paleosols have flat carbon isotopic profiles due to soil mixing (Chido of Fig .5). Preservation of such carbon-cycling signatures known from modern soils within different pedotypes gives additional evidence for paleosol classification and interpretation (Bestland and Krull 1999).

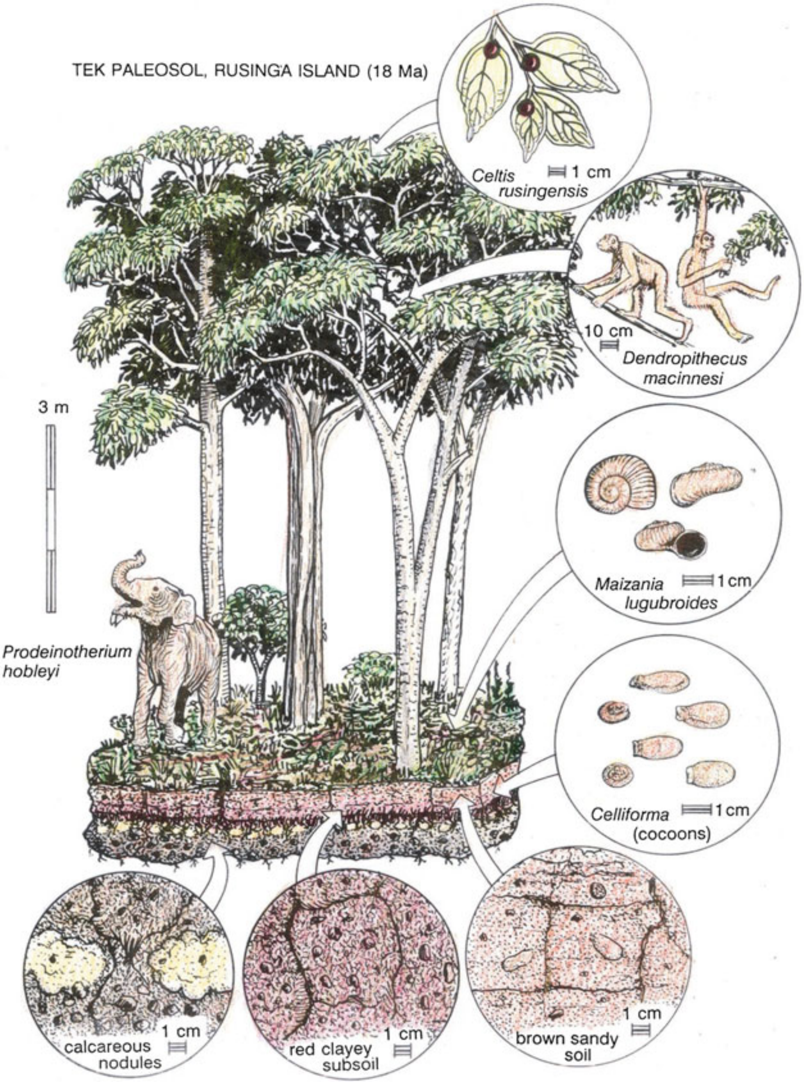

Fig. 4 Reconstruction of the Tek paleosol from the 18 Ma Hiwegi Formation of Rusinga Island, Kenya [Data from Retallack et al. (1995)]

Paleosols as Proxies of Paleoprecipitation

Climatic zonation of soils was a key element in the Russian origins of soil science (Jenny 1941), and a variety of relationships between particular soil features and climatic variables can be applied to East African paleosols in order to reconstruct paleoclimate. For example, depth to carbonate horizon (*D* in cm) is related to mean

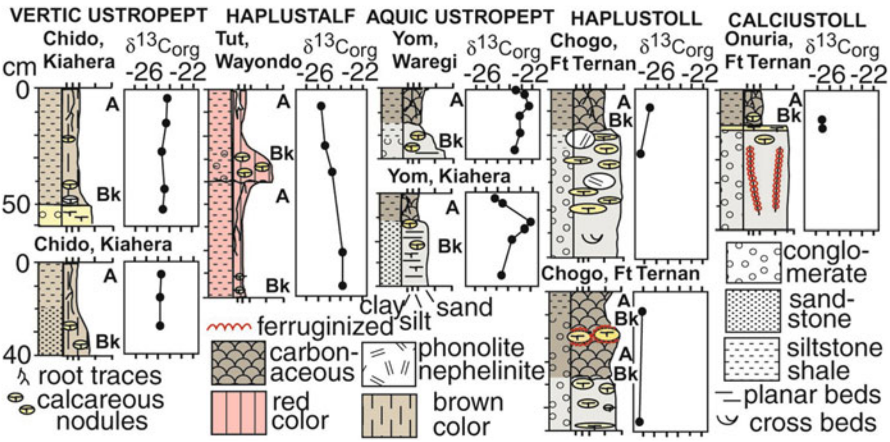

Fig. 5 Carbon isotopic ($\delta^{13}C_{org}$) depth profiles of Kenyan Miocene pedotypes, showing strong surface humification in grassland paleosols (Chogo and Onuria pedotypes), subsurface humification in Alfisols (Tut), and mixing in vertic Inceptisols (Chido). Carbon isotopic data is from Bestland and Krull (1999) and Cerling et al. (1997a), and paleosols are described by Retallack (1991a), Retallack et al. (1995), and Bestland and Krull (1999)

annual precipitation (*P* in mm) by a formula from Retallack (2005). This depth can be corrected for compaction due to overlying sediment using geological estimates of overburden and standard formulae (Sheldon and Retallack 2001). Also related to mean annual precipitation (*P*) is nutrient base content ($C = Al_2O_3/(Al_2O_3 + CaO + MgO + Na_2O)$ in mol) of soil Bt horizons by a formula from Sheldon et al. (2002).

Chemical weathering also alters the mineral content of soils, especially their clay minerals, which begin as smectites and then lose cationic bases with further chemical weathering to become kaolinite (Retallack 2001). This indication of paleoprecipitation works best with noncalcareous soils, which are found in climates receiving more than 1,000-mm mean annual precipitation (Retallack 2005). In East Africa today, smectite is dominant in soils receiving less than 1,200-mm mean annual precipitation, and kaolinite dominant in wetter climates (Mizota et al. 1988). Thus, noncalcareous, smectitic soils define a limited paleoclimatic window of 1,000–1,200-mm mean annual precipitation.

A new compilation of Kenyan paleoprecipitation over the past 20 million years (Fig. 6b) includes previously published data on African depth to Bk (Wynn 2001, 2004a,b; Wynn and Retallack 2002; Retallack 2001b; Retallack et al. 2002), and paleosol chemical (Retallack et al. 1995, 2002; Bestland 1990; Retallack 1991a; Wynn and Retallack 2002) and clay mineral composition (Retallack 1991a; Behrensmeyer et al. 2002), as well as published inferences from size and shape of fossil leaves (Jacobs 2002). This compilation is limited to data from around Lake Victoria for the early-middle Miocene, the Tugen Hills for the mid-late Miocene, and the Turkana Basin for the Miocene to Quaternary. The geological time scale is from radiometric dating of these various fossil primate sites (Deino et al. 1990;

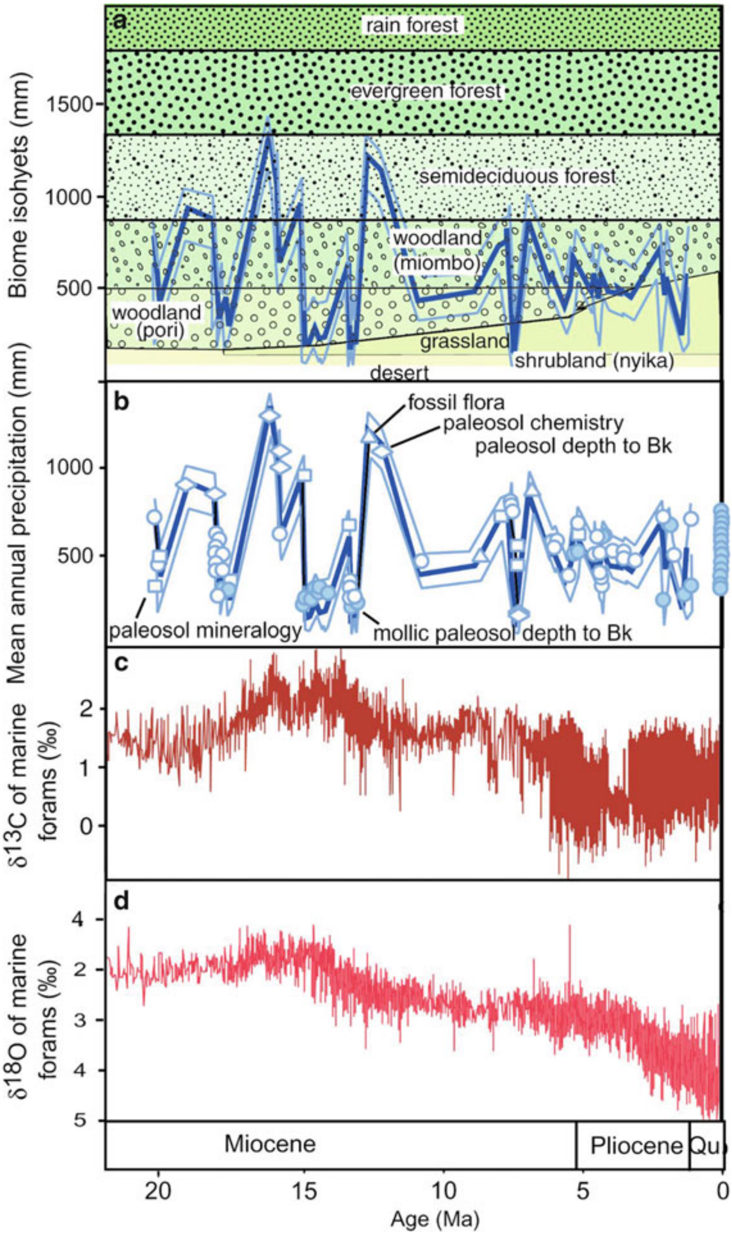

Fig. 6 A 20 million year record of vegetation (**a**) and paleoprecipitation (**b**) from Kenya, compared with carbon (**c**) and oxygen (**d**) isotopic composition of marine foraminifera. Paleoprecipitation data from paleosols (**b**) is from depth to carbonate (*open circles*), clay minerals (*diamonds*), and chemical composition (*squares*) after Retallack (1991a), Retallack et al. (1995, 2002), Wynn (2001, 2004a, b), and Wynn and Retallack (2002). Paleobotanical estimates from Jacobs (2002) and Jacobs and Deino (1996). Modern vegetation precipitation limits are from Anhuf et al. (1999)

Retallack 1991a; Jacobs and Deino 1996; Behrensmeyer et al. 2002; Hill et al. 2002; Pickford et al. 2006).

These new data reveal not just one Neogene aridification event at about 7 Ma, as has long been implied by the "Tertiary pluvial hypothesis" (Leakey 1952), the "Miocene lake hypothesis" (Kent 1944), the "Miocene rain forest hypothesis" (Andrews and Van Couvering 1975; Andrews 1996), and the "Late Miocene grassland hypothesis" (Cerling 1992; Cerling et al. 1997a,b). These theories had already been discredited by discovery of earlier Miocene desert dunes, shrubland snails, alkaline lakes, open-country grasses, grazing mammals, and grassland paleosols in East Africa (Pickford 1986a, 2002a; Retallack et al. 1990, 2002).

Instead the data (Fig. 6) reveal a Neogene paleoclimatic roller coaster of at least nine dry spells with intervening wet periods, of which humidity spikes at 16 and 13 Ma were the wettest of the last 20 million years. This new paleoprecipitation curve is similar to paleotemperature variations for Africa inferred from north-south oscillation through time of Ethiopian and Palearctic biogeographic realms (Pickford 2002a) and from paleoclimatic transfer functions from East African mammal assemblages (Retallack 2012). These new data are also similar to foraminiferal oxygen isotope curves from the deep sea (Zachos et al. 2001), commonly used as a basis for evaluating human evolution in Africa (de Menocal 2004), but the match is not precise (Fig. 6b,c). A general trend of extreme and volatile middle Miocene values, but subdued late Miocene to Quaternary values, is evident from both isotopic and paleosol data. The paleosol record reveals much greater variation in rainfall than would be inferred from carbon isotopic values of marine foraminifera, which are damped by global oceanic mixing with time lags of several thousand years. More profound damping is seen in oxygen isotopic values of marine foraminifera, which show a long-term increase unlike local rainfall and foraminiferal carbon records. This increase is plotted on reversed axes in Fig. 6d, because it has been interpreted as a long-term temperature decline (Zachos et al. 2001), but part of this long-term trend is due not just to temperature but to water recycling with plate tectonics (Veizer et al. 2001). The global oxygen isotope record also shows an increase after 3 Ma due to continental icecap sequestration of isotopically light oxygen, in addition to temperature effects (Zachos et al. 2001). Despite these problems, the East African paleosol record and global isotopic records present a very different concept of climatic variation experienced by our distant ancestors than the past idea of a seminal Late Miocene climatic event. Instead of a single origin of humanity at a turning point of environmental change, the new record implies rather that our lineage responded to a gauntlet of changing conditions with a variety of adaptations (Table 1), as discussed later.

Paleosols as Trace Fossils of Ecosystems

Australopithecus afarensis is known from body fossils, such as the partial skeleton "Lucy" (Johanson et al. 1982), as well as from trace fossils, such as the footprints of Laetoli (Leakey and Harris 1987). The soils of *A. afarensis* also are known,

Table 1 Geological age of African climatic events, selected adaptations, and hominoid diversity (*D*), origination (*O*), and extinction (*E*)

Age (Ma)	Hominoid adaptations and extinctions	*D*	O	E
20.2 dry	Robust mandible for hard food (*Rangwapithecus*)	10	9	0
19.1 wet	Low cusp molars for folivory (*Nyanzapithecus*)	5	0	5
17.7 dry	Thick enamel for hard food (*Afropithecus*)	6	1	2
16.1 very wet	Short back for suspension (*Proconsul (“Morotopithecus*”))	4	3	6
14.9 very dry	Adducted hallux for ground walking (*Equatorius*)	7	4	2
12.6 very wet	Thin enamel molars for soft food (*Otavipithecus*)	2	2	5
10.7 dry	Large size for ground feeding (*Samburupithecus*)	3	3	0
8.6 wet	Ape extinction with monkey radiation (*Microcolobus*)	1	1	3
7.5 very dry	Knuckle walking for ground (*Pan-Gorilla* ancestors)	1	1	1
6.8 wet	Upright stance for nest provisioning (*Orrorin*)	1	1	1
5.4 dry	Small incisiform canines for hard food (*Ardipithecus*)	3	1	2
4.2 wet	Flat face for stereoscopic vision (*Kenyanthropus*)	1	1	3
2.5 dry	Large molars for hard food (*Paranthropus*)	6	4	2
2.1 wet	Small molars for soft food (*Homo habilis*)	3	0	4
1.8 dry	Long legs for endurance running (*Homo ergaster*)	5	3	2
1.7 wet	Occipital bun for competition (*Homo erectus*)	4	0	3
1.0 dry	Globular brain for generalist roles (*Homo antecessor*)	4	2	1
0.1 wet	Magdalenian tools and culture (*Homo sapiens*)	1	1	4

especially at the “first family” site near Hadar, Ethiopia (Radosevich et al. 1992; Behrensmeyer 2008). Here a troop of at least 13 individuals, young and old, died, rotted, and were partially disarticulated, before being interred in flood deposits on a crumb-structured soil of grassy streamside woodland (Fig. 7). The paleosol is not only a matrix to the bones but a trace fossil of their ecosystem. Furthermore, paleosols by definition are in the very place they formed, not redeposited. Unlike the skeleton of “Lucy,” found in the sandstone of a former river channel (Johanson et al. 1982), and thus transported some distance from its natural habitat, the first family was found where it died and had lived (Radosevich et al. 1992; Behrensmeyer 2008). Thus, paleosols give a finer resolution of primate paleoenvironments in time (Fig. 6) as well as space (Fig. 7).

The various paleosols containing Miocene ape fossils in southwest Kenya can also be used to constrain their habitats (Fig. 8). The fragmentary and weathered nature of most of these fossils is evidence that they accumulated through natural processes of death and decay on the paleosols in which they are found (Pickford 1986a). The great diversity of fossil apes in this region (Gommery et al. 2002; Harrison 2010; Ward and Duren 2002) is in contrast to the low diversity of great apes today (Fleagle 1998), leading to the idea that Miocene apes, defined from apelike dentition, were ecologically more like monkeys today (Andrews 1996). Analysis of their occurrence in paleosols shows that there was some ecological separation of different species to different soil types, but still high diversity within a soil type (Fig .8). In the 20 Ma sites of Koru and Songhor, for example, one very

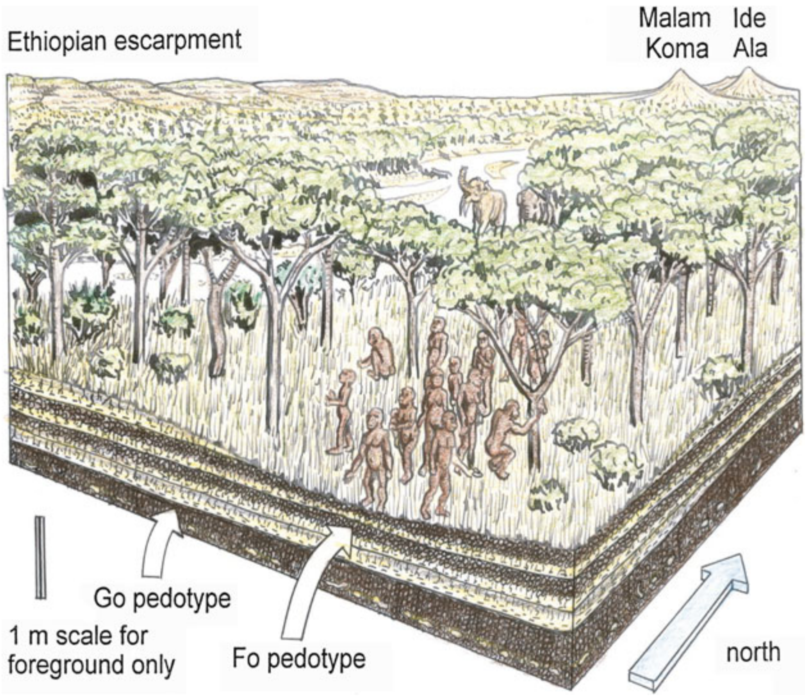

Fig. 7 Reconstruction of paleosols at the "First Family site" for *Australopithecus afarensis* at Hadar [Data from Radosevich et al. (1992)]

large taxon (*Proconsul major*) shows little habitat specificity through a variety of tropical dry forest habitats, but small taxa (*Kalepithecus*, *Micropithecus*) are found in upland soils and larger taxa (*Proconsul*, *Rangwapithecus*, *Dendropithecus*, *Limnopithecus*) remained in lowland forests closer to water. One paleosol type (Kiewo pedotype) has as many as six taxa including a large ground species (*Proconsul major*), three likely suspensory feeders (*Limnopithecus evansi, L. legetet, Dendropithecus* from small to large) and two likely overbranch feeders (*Proconsul africanus*, *Rangwapithecus*, from small to large). The contrasting sizes and other differences between these taxa suggest niche partitioning of forest canopy tiers.

Diverse catarrhine communities persisted into the dry woodland landscapes of Rusinga Island at 17.8 Ma, when paleosols with the crumb peds and iron-manganese nodules of dambo grasslands (Yom pedotype) appear, but are rare and barren of primate fossils (Retallack et al. 1995). Other evidence for grasslands of about the same age is abundant bunch grasses at the Ugandan fossil site of Bukwa (Pickford 2002b). Yom paleosols of dambo grassland are much more common by 14.7 Ma on Maboko Island (Retallack et al. 2002), where they contain abundant vervet-like monkeys (*Victoriapithecus*: note change of scale for this exceptional collection in Fig .8). These seasonally inundated grasslands of dry climates were

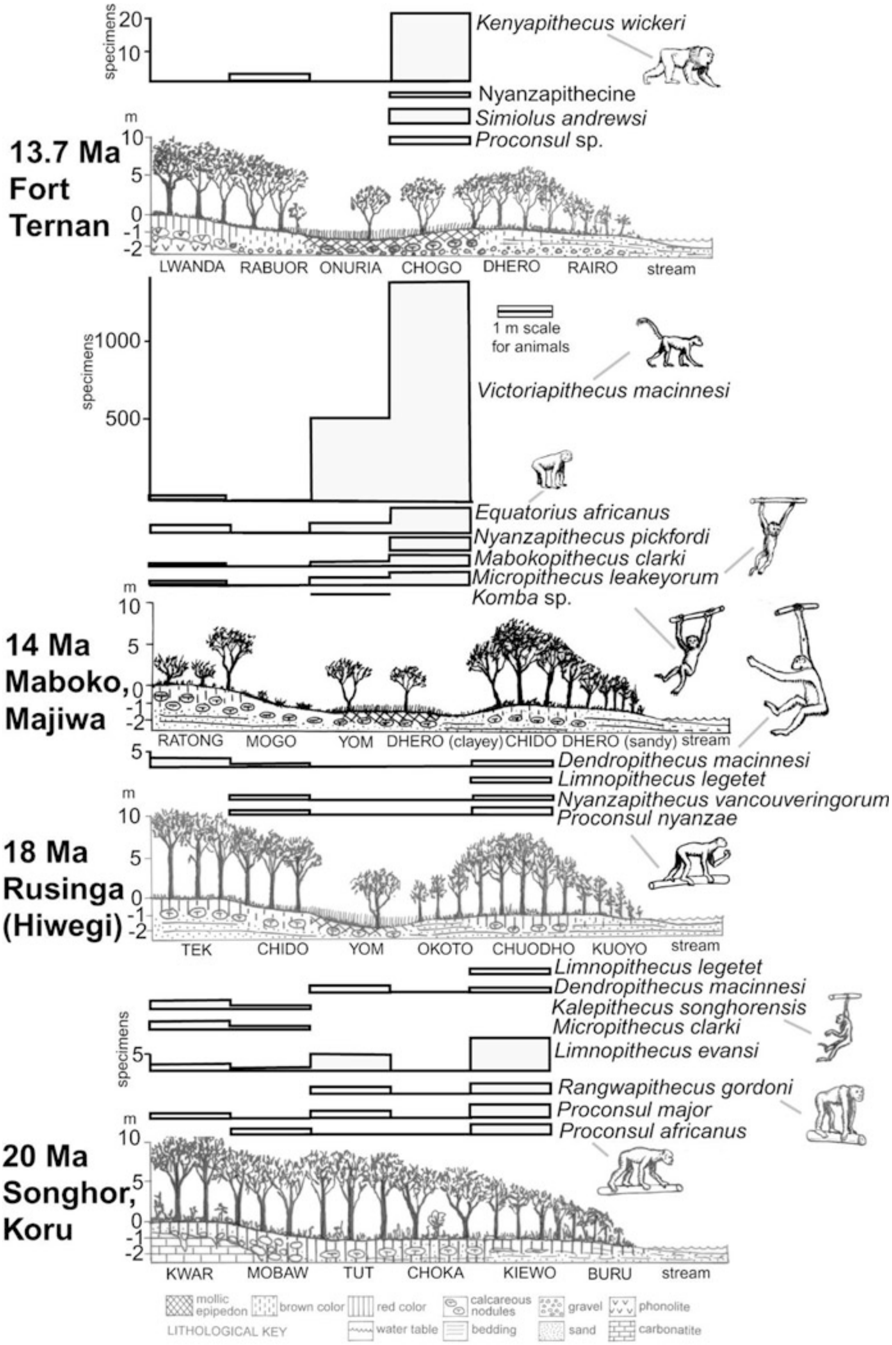

Fig. 8 Paleosols of Miocene apes from southwestern Kenya [Data from Retallack (1991a) with taxonomy after Retallack et al. (2002), Ward and Duren (2002), Harrison (2010)]

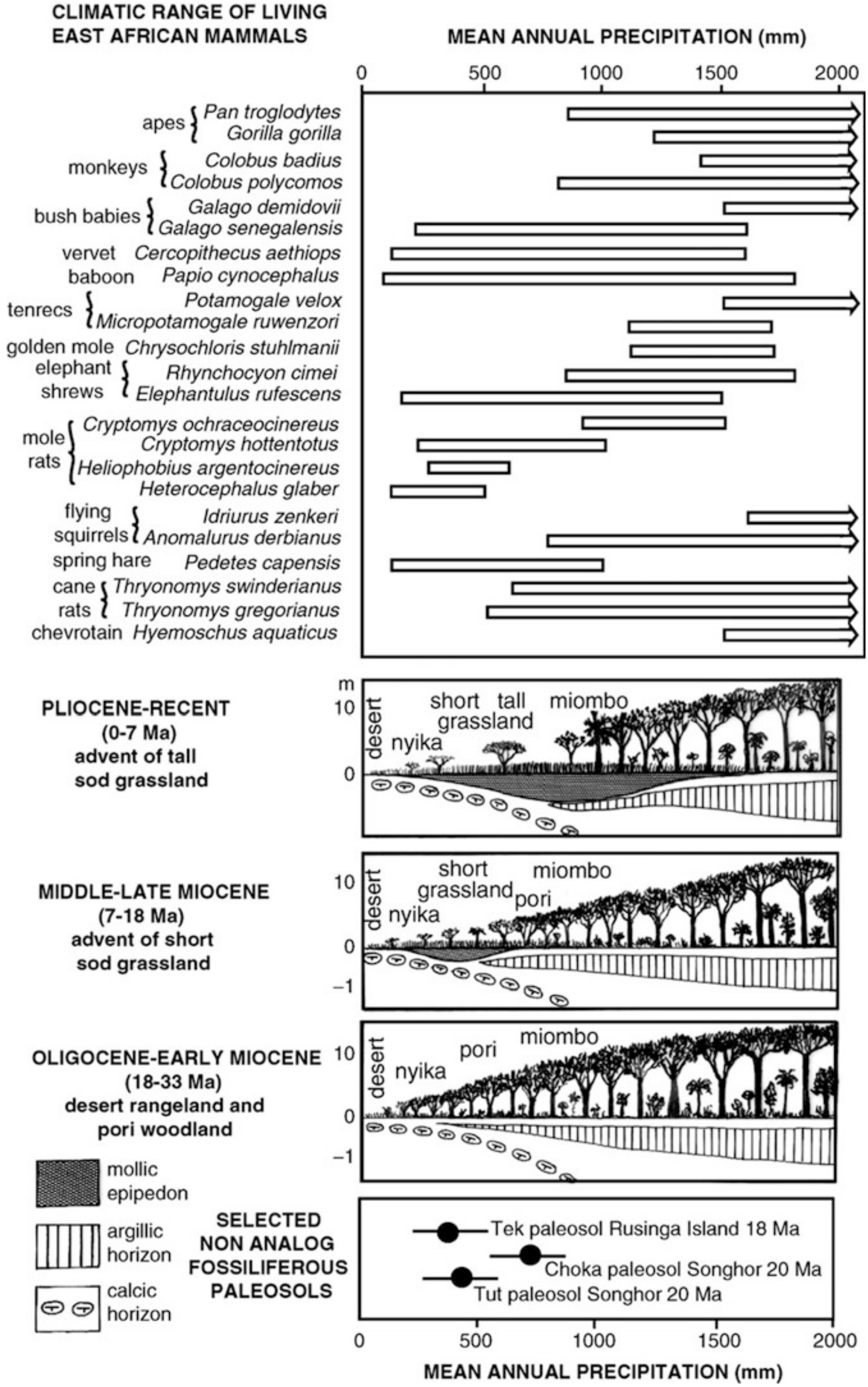

Fig. 9 (continued)

not encouraging to fossil apes, which were more common in riparian woodlands (*Nyanzapithecus*, *Mabokopithecus*, and *Micropithecus* of Dhero paleosols). More wide ranging was *Equatorius*, found in both riparian woodland (Dhero) and nyika shrubland (Ratong), which it exploited more effectively than other apes because of its thick enameled, large molars useful for tough foods (Martin 1985) and its macaque-like limbs and feet (McCrossin et al. 1998). A similar pattern of wide ranging *Kenyapithecus* and forest-dependent other apes (*Simiolus*, *Proconsul*, Nyanzapithecine) persisted in grassland mosaics of Fort Ternan and Kapsibor at 13.7 Ma (Pickford et al. 2006), when well-drained short-grass, wooded grassland was widespread. The appearance of grasslands that was encouraging for victoria-pithecine ancestors of vervets and colobines was not so hospitable to apes, which remained rare components of the fossil fauna.

Reconstruction of rainfall from paleosols implies also vegetation belts (Fig .6a), by comparison with Holocene climatic ranges of plant formations (Anhuf et al. 1999). There was rainforest in central Africa during the past 20 million years as indicated by rare finds of fossil plants (Bancroft 1932, 1933), but evidence of rain forest has not yet been found in the East African areas yielding hominoid fossils (Retallack 1991a; Jacobs 2002). Paleobotanical interpretations (Fig .6a) are well in accord with indications of vegetation from paleosol classification, profile form and root traces (Retallack 1991a), as evidence that the climatic range of most vegetation types did not change over the past 20 million years.

An exception is the evolution of grasslands, which expanded their climatic range to displace extinct kinds of woodlands (Figs. 6 and 9). There is not yet any East African evidence of grasslands before 17.8 Ma, when crumb-textured, brown, simple (A-Bk) profiles of dambo were rare at Rusinga Island (Retallack et al. 1995) and bunchgrasses grew luxuriantly at Bukwa (Pickford 2002b). Well-drained, short-grass, sod-grasslands were widespread by 14.4 Ma (Retallack 1991a; Retallack et al. 2002) and well-drained, tall-grass, sod-grasslands expanded their climatic range considerably by 7 Ma (Wynn 2004a, b). Grasslands were a newly coevolved ecosystem of the Cenozoic, with grasses uniquely suited to grazing by virtue of their intercalary meristems, modular growth, basal tillering, and sod formation, and grazers uniquely suited to coarse grassy fodder by virtue of their wide muzzles, hypsodont teeth, and hard hooves (Retallack 2001a). A world without grasslands was transformed over some 20 million years to a Plio-Pleistocene world with grassland covering at least a quarter of the land surface. Holocene humans spread grassy agroecosystems to almost all parts of the world (Retallack 2001a). Neogene expansion of grasslands within the paleoclimatic belt

Fig. 9 A scenario for stepwise evolution of East African grasslands with modern precipitation tolerances of African mammals related to those found fossilized in paleosols (Tut, Choka, Kwar) of pori woodlands that preceded the expansion of grasslands. The advent of grasslands disrupted formerly overlapping ranges of apes, bush babies, flying squirrels, mole rats, and spring hares. Climatic ranges of modern mammals are from Kingdon (1971, 1974a, b, 1979) and of paleosols from Retallack (1991a), Retallack et al. (1995)

Table 2 Comparison of extinct pori woodland with extant East African vegetation

Local name	Pori	Miombo	Nyika	Savanna
Vegetation	Dry woodland	Dry woodland	Dry bushland	Wooded grassland
Key genera	*Celtis*	*Brachystegia*	*Acacia*	*Combretum*
Floral origins	Zambezian	Zambezian	Zambezian	Eurasian
Spinosity	Unarmed	Unarmed	Spinose	Spinose
Leaf set	Semideciduous	Deciduous	Deciduous	Deciduous
Fruit size	Large	Large	Small	Small
Snails	*Cerastua*	*Limicolaria*	*Achatina*	*Pupoides*
Snail origins	Somalian	Somalian	Somalian	Somalian
Mammals	Apes, rodents	Antelope	Antelope	Antelope
Ungulates	*Walangania*	*Aepyceros*	*Tragelaphus*	*Connochaetes*
Primates	*Proconsul*	*Cercopithecus*	*Papio*	*Papio*
Mammal origin	Zambezian	Zambezian	Zambezian	Eurasian
Fire frequency	Low	High	High	High
Soil organics	Low	Low	Low	High
Soil fertility	High	Low	Low	High
Soil type	Alfisol	Oxisol, Vertisol	Aridisol	Mollisol, Vertisol
Parent material	Volcanic	Granitic	Granitic	Volcanic

roughly defined by the 300–750 mm per annum isohyet enabled grasslands to capture the planetary modal rainfall belt and most fertile soils, with consequences for global change including a significant contribution to global cooling (Retallack 2001b).

Before the expansion of the grasslands, an extinct woody vegetation occupied their climatic range (Fig. 6). These extinct dry woodlands can be called pori (Table 2), from a Hadza word for bush (Woodburn 1968). A good example of a pori ecosystem is the Tek paleosol of Rusinga Island (Figs. 3 and 4), which has yielded fossil primates and other mammals, snails, and plants (Pickford 1995; Retallack et al. 1995). Other examples of pori ecosystems include Tut, Choka, and Kwar pedotypes of Songhor and Koru dated at 20 Ma (Retallack 1991a). From the soil perspective, these paleosols have no clear modern analog, because they are red and clayey, with large root traces and blocky structure like woodland soils, yet have shallow calcareous horizons like those found in modern African semiarid to subhumid grassland soils. Modern African soils with such shallow carbonate have very different crumb structure, fine root traces, and dark brown organic-rich surface horizons from abundant grasses.

From the paleoanthropological perspective, these ancient communities have no modern analogs, because they have so many fossil hominoids, as many as six species in the Kiewo pedotype (Fig. 8). No community has so many species of hominoids today. Nor do modern hominoids live in such dry climates. Mt. Assirik in Senegal with 956 (854–1224) mm mean annual precipitation is the driest climate with chimpanzees (Kappelman 1993), although Kingdon (2003) gives anecdotes of chimpanzees in wooded grassland. It is now clear that Miocene apes filled a variety of niches like those today filled by vervets, baboons, and colobines as well as apes (Retallack et al. 2002). Pori ecosystems such as the Kwar paleosol at Koru (20 Ma) also show peculiar associations of other mammals, including a mix of dry climate taxa, such as mole rats (*Bathyergoides*), with wet climate taxa such as flying squirrels (*Paranomalurus*), giant elephant shrews (*Miorynchocyon clarki*), tenrecs (*Protenrec tricuspis*), golden moles (*Prochrysochloris miocaenicus*), and chevrotains (*Dorcatherium songhorense*: Retallack 1991a). Similarly, the Tut and Choka paleosols at Songhor (20 Ma) and Tek paleosols on Rusinga Island (17.8 Ma) have wet climate flying squirrels and tenrecs as well as dry climate mole rats and spring hares (Retallack 1991a; Retallack et al. 1995). These nonanalog combinations of fossil mammals can be explained by a theory of evolutionary replacement of pori with grassland within semiarid to subhumid regions. Before the advent of grasslands, woody vegetation became smaller in stature and biomass from wet to dry regions (Retallack 2012). This continuum was disrupted as grasslands evolved to usurp the climatic range of pori woodland. Grasslands expanded their range to create a biogeographic divide between nyika shrubland and miombo woodland (Fig. 9).

Fossil primates of East Africa not only coped with changing mixes of animals, but with changing climate and vegetation (Fig. 6). Wynn (2004b) has introduced the concept of evolutionary entropy to explain effects of climate and vegetation change on hominoid diversity. Climatically dry episodes encouraged grassland mosaic environments with a more varied landscape of open grassland and local woodland, and thus greater landscape disorder or negentropy. Wet episodes of forest vegetation presented more uniform landscapes of higher entropy. Compilation of

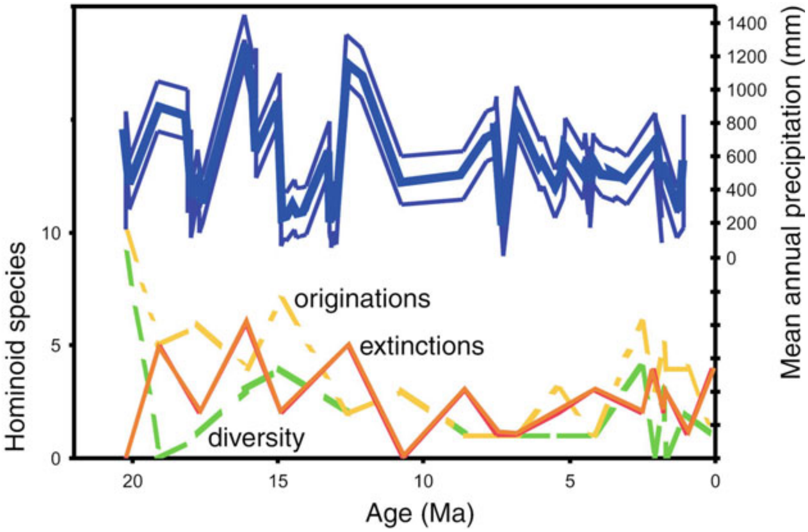

Fig. 10 Mean annual precipitation and hominoid diversity, extinctions, and originations in East Africa over the past 20 million years. The paleoprecipitation curve is from Fig. 6. Hominoid data is from Pickford (1986b, 1987), Ward and Duren (2002), and Carroll (2003)

hominoid diversity, originations, and extinctions (Table 1, Fig. 10) supports the view that dry episodes correspond with diverse primates, whereas wet episodes lead to extinctions, particularly of specialized arid-adapted taxa. The concept of ecosystem entropy in hominoid evolution is similar in some respects to Vrba's (1999) "turnover pulse hypothesis," but ecosystem entropy presents diffuse and long-term selection pressures, rather than episodic crises or "turnover pulses." Recent compilations of mammalian data from the Turkana region do not show such crises (Bobe et al. 2002), revealing instead an oscillating diversity compatible with less synchronized selection by ecosystem entropy.

A major caveat for such theories is the generally inferior fossil record of climatic wet phases, because their soils and sediments are noncalcareous and so not favorable to the preservation of bone (Retallack 1998). There is still no primate fossil record from paleoclimatic wet phases of the early Miocene, but there are discoveries of wet climate human ancestors from 13 Ma (Hill et al. 2002), 6 Ma (Brunet et al. 2002; Galik et al. 2004), and 4–3 Ma (Carroll 2003). The soil-taphonomic bias against wet climate fossils makes the search difficult, not impossible (Peterhans 1993).

Each fluctuation in climate and vegetation presented new crises and opportunities to primates. The correlation of climatic events with critical adaptations presented here (Table 1) is only an outline of a new research agenda, to be fleshed out with further studies of the critical intervals. The late Miocene paleosols and primate fossils of the Tugen Hills, for example, remain very poorly known compared with those of the Lake Victoria and Turkana basins. Nevertheless, there are general themes apparent from this compilation. We did not evolve from apes in one seminal event, but by a protracted process of growth and pruning of our evolutionary tree. Some specialized features such as procumbent incisors at 18 Ma evolved in dry grassy woodlands, but did not survive succeeding forest expansions (McCrossin and Benefit 1997). Some specialized features such as long arms by 20 Ma for suspensory locomotion in forests did not persist through succeeding grassland expansions (Harrison 2010). Other forest adaptations such as a short stiff back by 16 Ma (Pickford et al. 1999), erect stance by 6 Ma (Senut et al. 2001; Galik et al 2004), and flat face by 3.5 Ma (Leakey et al. 2001) proved advantageous in the long term, just as did grassland adaptations, such as thick enamel by 18 Ma (Martin 1985; McCrossin and Benefit 1997), adducted hallux by 14.7 Ma (McCrossin et al. 1998), and long legs for endurance running by 1.8 Ma (Bramble and Lieberman 2004). Although each of these ideas could be debated individually, the general concept of human evolution as a generalist path through a gauntlet of environmental challenges (Potts 1996) is increasingly supported by a burgeoning fossil record (Carroll 2003). There will always be a need for dating and finding more human ancestor fossils, but paleosols now provide new evidence of evolutionary selection pressures with high temporal and spatial resolution.

Past hypotheses of a Miocene pluvial, lake and rain forest (Kent 1944; Leakey 1952; Andrews and Van Couvering 1976; Andrews 1996) and late Miocene grassland (Cerling 1992; Cerling et al. 1997a, b) find a counterpart in long-standing theories linking late Miocene evolution of human upright stance or large brains with hunting prowess (Darwin 1872), vigilance against predators (Dart 1926), manipulation of small seeds (Jolly 1970), minimization of sun exposure (Wheeler 1984), long-distance walking (Rodman and McHenry 1980) or running (Bramble and Lieberman 2004), squat feeding on the ground (Kingdon 2003), or moving between scattered fruiting bushes (Sanford 2003). Forest explanations of upright stance allowing erect-back climbing (Tuttle 1981), hands free to care for premature infants (Lovejoy 1981), phallic display to females (Tanner 1981), or intimidation displays to rivals (Jablonski and Chaplin 1993) move the event back into the "Miocene rain forest" (of Andrews and Van Couvering 1975; Andrews 1996), for which there is little evidence at hominoid sites in East Africa (Fig. 6a). All these views can be reassessed in light of the improved record of East African paleosols, which suggests that there were many alternating habitats in East Africa, not just one seminal environmental shift. Darwin's (1872) idea that erect stance was linked to tool use and brain expansion has been out of favor since the discovery of "Lucy," when it became clear that erect stance preceded tool use and brain expansion by millions of years (Johanson et al. 1982). Erect stance now appears to have occurred in wooded habitats by 6 Ma (Pickford and Senut 2001; Vignaud et al. 2002; White et al. 2009), perhaps selected by the use of hands in nest provisioning (Lovejoy 1981). We are a mosaic of a complex evolutionary history and no longer need to settle for simple or single allegories of human evolution.

Conclusion

There is a copious and informative fossil record of soils at most of the fossil ape and human ancestor sites in Africa, and study of these paleosols is now giving important insights into the long evolutionary career of our ancestors. The primate evolutionary radiation of the Neogene has been a long saga of changing habitats and adaptations. The fossil record of soils now allows us to address its complexity on a scale appropriate to primate home ranges and to recognize nonanalog habitats of the past. Our distant ancestors have run an evolutionary gauntlet of changing vegetation and climate that has spawned many evolutionary innovations, some of them lasting only to the next shift in climate and vegetation, but others of them proven to be of lasting value.

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Dental Adaptations of African Apes
- ▶ Fossil Record of Miocene Hominoids
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Quaternary Geology and Paleoenvironments
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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Quaternary Geology and Paleoenvironments

John A. Van Couvering

Contents

Abstract

The Quaternary is defined by its unusual climate, which was originally characterized as advances and retreats of continental ice sheets in the Northern Hemisphere. The earliest such glaciation, at about 2.6 Ma, is now recognized as one step in a worldwide cooling trend that began some 38 million years ago when the world ocean first felt the effect of the great Antarctic ice sheet. With the loss of ocean warmth, the cycles in the Earth's orbit that affect the solar radiation reaching the surface have had a steadily increasing influence on world climate, and glacial-interglacial swings have grown progressively stronger. The earliest *Homo* appears in the fossil record at the same time that the more extreme Quaternary climate changes began to increase grasslands in Equatorial Africa, giving wider opportunity for bipedal, stone-wielding scavengers.

J.A. Van Couvering (✉)
Micropaleontology Press, Queens, NY, USA
e-mail: vanc@micropress.org

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Introduction

The Quaternary – the final hour of geological time – is a highly distinctive interval with unique attributes, even if we refrain from giving undue significance to the evolution of genus *Homo* within its limits and even if we treat the consequences as being outside the range of a geological review.

The individuality of this time period was first recognized by Giovanni Arduino, who in 1759 had proposed a Primary (igneous-metamorphic) and Secondary (lithified and folded) organization of formations as seen in the geology of the Apennines (Arduino 1759). As a side note, he recognized an informal third subdivision of "low mountains and hills of sand and gravel" and a fourth and final subdivision – that of "earth and rocky materials and alluvial debris." In 1810, the third subdivision gained the title of Tertiary (actually, *tertiaire*) in Alexandre Brongniart's description of strata younger than the massive Late Cretaceous chalks of the Paris basin. Marcel de Serres, after initially recognizing the fourth of Arduino's subdivisions merely as *quatrième formation d'eau douce* (in Creuze de Lesser 1824, p. 174), in 1830 used the term *quaternaire* for such superficial deposits. He subsequently (de Serres 1855) claimed to have thereby invented Quaternary as a lithostratigraphic term, but the honor goes, somewhat unjustly, to Desnoyers (1829), who proposed to call all the nearly horizontal, relatively unconsolidated younger strata of the Loire and Rhône basins *Quaternaire ou Tertiaire récent*, as follows:

(3) *Récent*
(2) *Diluvium*
(1) *Faluns de Touraine, la molasse suisse*, *et le Pliocène marin de Languedoc*

In this way, the first use of the term Quaternary referred to strata as old as the Lower Miocene! This was partly because *tertiaire* in France was initially applied only to the Lower Cenozoic strata of the Paris basin and perhaps also because the southern French Miocene, to which Desnoyers referred, was much less indurated or deformed than the coeval Italian Miocene which Arduino placed in his third subdivision. However, the earlier usage of de Serres, which he restated in 1830 in confining Desnoyers' *quaternaire* to "diluvium" only (de Serres 1830), was more in line with that of Arduino, and it established the modern meaning of the term. The purely lithological concept of Quaternary is still a strong tradition in geology, and many relatively unconsolidated, unfossiliferous formations are mapped as "Quaternary terrace" or "Older Quaternary alluvium" with no further attempt at formally dating them.

A second defining concept for Quaternary, that of a period equivalent to the span of human existence, was also suggested by de Serres (1830), who asserted that early man had lived during the deposition of the Quaternary "diluvium." The first major treatise on the *Terrain quaternaire ou diluvien* (Reboul 1833) thus proposed that this time interval be considered as the "Période anthropiénne." Other writers called it the "Periode homozoique" (Vezian 1865) and "Terrain humaine" (Mercey 1874). At the International Geological Congress of 1888 in Great Britain, Jean Gaudry, with the approval of Joseph Prestwich and Albert De Lapparent, made the proposal that mankind – represented in particular by artifacts – was the characteristic element of the Quaternary and that this justified its separation from the Tertiary.

A different logic for defining the final part of the geological record was outlined by Charles Lyell, who never referred to "Quaternary." Instead, he began with formally defining the term Pliocene, already in use as a general descriptive word for fossils of relatively young age (e.g., Desnoyers 1829), with reference to certain marine formations in Great Britain, the Lowlands, and Italy in which 50 % or more of the molluscan species they contained as fossils survived to the present day (Lyell 1833, p. 61). Within this interval, he recognized "Newer Pliocene" formations with at least 90 % of the surviving species.

In 1839, Lyell replaced "Newer Pliocene" with "Pleistocene," again without any reference to Quaternary (Lyell 1839). At almost the same moment, Agassiz (1838) made the bold suggestion that the European continent had been invaded by great lowland glaciers during the Quaternary. By this time, it was already widely understood that the continental Quaternary deposits and "younger Pliocene" marine deposits were roughly coeval. It took very little time for Forbes (1846), after noting that the molluscan faunas to which Lyell had referred in setting up the Pleistocene were adapted to a colder climate than those of the Pliocene, to conclude that the marine Pleistocene, like the continental Quaternary, should be recognized as ". . . the time distinguished by severe climatal conditions throughout the great part of the northern hemisphere" (Forbes 1846, p. 402).

"The first glaciation," however, was still only one of a variety of criteria that were cited as definitions for the base of the Quaternary (and/or Pleistocene) at the middle of the twentieth century, as follows:

Paleoanthropologists: first evidence of man or tools
Paleoclimatologists: first (major) global cooling or glacial advance
Vertebrate paleontologists: first joint occurrence of *Equus*, *Leptobos*, and *Elephas* in Eurasia
Marine invertebrate paleontologists: first occurrence of cold-water species in late Neogene sediments of Mediterranean basin
Paleobotanists: first "glacial" floral association or exclusion of certain southern elements from European floras

To further complicate matters, each of these conceptual criteria could be and usually was interpreted locally, with often highly inconsistent results. In one very notable example (cf. Van Couvering 1997), the Quaternary community in North America, Western Europe, and China consistently placed the beginning of the Quaternary at the first appearance of glacially derived tillites or loess in temperate high plains sequences. On the other hand, Russian and East European workers held that Forbes' definition of "fully glacial" conditions meant that the Pleistocene – and thus the Quaternary – began when the first continental ice sheet completely covered Northern Europe during the Menapian glacial maximum, at the same time as the first appearance of modern cold-climate biota (Nikiforova 1997). It was well recognized that these concepts differed markedly in age, even before modern dating confirmed that the first was related to a cold period close to the Gauss/Matuyama boundary, at ca. 2.5 Ma, while the second was applied to the beginning of the modern glacial-interglacial climate at 0.9 Ma, just subsequent to the Jaramillo subchron (cf. Lourens and Hilgen 1997). Such special pleading, however, was countered, if not silenced, at the 18th (London) International Geological Congress in 1948. At this Congress, the Temporary Committee for the Study of the Pliocene/Pleistocene Boundary recommended that the boundary "... should be based upon changes in marine fauna, since this is the classical method of grouping fossiliferous strata" (King and Oakley 1950). In other words, the paleoclimatic and other special attributes of the Quaternary, which various groups had cited in their conceptual definitions, were irrelevant to its meaning as the youngest Period, and uppermost System, in the geological time scale.

If the Committee had done no more than this, it would have earned its laurels. Under the influence, however, of the new "Cambridge school" of analytical stratigraphers, led by W. Brian. Harland, the Committee made a bold step onto new ground that has since revolutionized chronostratigraphy and made its boundaries accessible to modern techniques used in biostratigraphy, magnetostratigraphy, and geochronology. This was the first enunciation of the principle informally called the "golden spike" (cf. Ager 1973), which we now identify as the GSSP or Global Boundary Stratotype Section and Point – i.e., not only that a chronostratigraphic boundary be typified in an appropriate marine section but also that it be anchored to a specific physical stratum. This was inherent, if not clearly stipulated in the Committee's recommendation that ". . . the Lower Pleistocene should include as its basal member in the type-area the Calabrian Formation (marine) together with its terrestrial (continental) equivalent the Villafranchian." Aside from the egregious and, as it turned out, mistaken inclusion of the significantly older Villafranchian, which seems to have been a sop to the nonmarine specialists on the Committee, this was the key element to pinning down this hitherto elusive boundary.

The new principle of a physical definition superseded the various "model" or conceptual criteria of the past, including climate-induced changes in the marine invertebrate fauna, although this fact was not clear to everyone at the time. In fact, the Committee itself justified its proposal by pointing to changes in the marine and continental faunas that were understood to coincide with the Calabrian in southern Italy. Nevertheless, such changes were merely supportive of the decision where to locate a physical pointraphic criterion that, once put in place, would stand apart from any theoretical model of past events. In so doing, they made the record of climate, fauna, or flora, irrelevant to the actual definition of the boundary, although such evidence was more significant than ever because of the greater precision demanded by reference to a single physical point in its correlation.

Modern Definition of the Quaternary: A Continuing Controversy

With attention thus focused on the Calabrian Stage, the question became one of its appropriate stratotypes for location of a fixed physical reference point, or "golden spike." In the original type section, as described by Gignoux (1913) at Santa Maria di Catanzaro, Calabria, the lower part of the section is not well exposed. In 1965 at the 7th (Denver) Congress of the International Union for Quaternary Research, better known as INQUA, it was proposed to fix the base of the Pleistocene at a better exposure about 40 km distant at Le Castella. To follow up on this question, in 1974 the International Geological Correlation Program launched IGCP Project 41, "Neogene-Quaternary Boundary," which was charged with comparing the suitability not only that of the sections at Santa Maria di Catanzaro and Le Castella but also that of a third seacliff exposure of Calabrian strata at Vrica, further to the east near Crotone. After it turned out that glacially lowered sea level during the early Calabrian had in fact created a hiatus at the base of the two shallow-marine sections at Santa Maria di Catanzaro and Le Castella (Colalongo et al. 1981), attention turned to the deeper-water section at Vrica, where a boundary point was chosen in a layer, now dated 1.81 Ma in the uppermost part of the Olduvai Event (Hilgen 1994; Gradstein et al. 2004), that makes the transition to typical Calabrian lithology and molluscan fauna in the Italian sequences. The Vrica boundary was approved in a joint meeting of IGCP Project 41 and INQUA in Moscow in 1985, and the formal proposal for this new identity of the Pleistocene was adopted by the IUGS (International Union of Geological Sciences) in 1986 (Cowie et al. 1986). The final report of IGCP Project 41 (Van Couvering 1997) reviewed the flood of studies on the Vrica boundary and its worldwide correlation.

The main problem with the Vrica-defined Pleistocene was that the cold-water episode that introduced "boreal visitors" such as the clam *Arctica islandica* into Calabrian faunas, as noted in the 1948 Commission's decision, was not the first glacial-climate cycle at the end of the Cenozoic. The marine community readily accepted the Vrica definition, because it could be precisely correlated in deep-sea cores on the basis of paleomagnetism, micropaleontology, oxygen isotopes, and (in later years) cyclostratigraphy (cf. Gradstein et al. 2004), and most continental paleontologists and paleoanthropologists were comfortable with the date as well. It was unacceptable, however, to the continental stratigraphers who dominated INQUA and who continued to use a paleoclimatic definition of Quaternary that was based on the earliest glacially derived lowland deposits in north temperate sequences. This was a criterion that the Vrica boundary, linked to Lyell's marine biostratigraphic definition, did not satisfy.

In May 2009, the IUGS ratified a proposal made by INQUA to the Quaternary subcommission of the International Commission on Stratigraphy, which was approved by the full ICS against the opposition of its Neogene subcommission (cf. Van Couvering et al. 2009). This proposal gave the Quaternary formal status as a System/Period in the standard geological time scale (Finney 2010), placing the lower (and only) boundary of the new unit at the base of the Gelasian Stage at San Nicolá, Sicily. This boundary, dated at 2.59 Ma, was selected because of its

Table 1 Quaternary terminology. Classic "ice age" names (*interglacials in italics*) in continental ice sheets of the Northern Hemisphere, coordinated with dated peaks in the oxygen isotope curve from deep-sea cores. Some names in the early Quaternary refer to generalized intervals in which individual advances and retreats were not easily distinguished in the field

North America	North Sea	Alpine	Peak AGE, Ma	Marine isotope stage (MIS)
	Flandrian		*0.017*	*MIS1*
Wisconsinian	Weichsel or Devensian	Würm	0.023	MIS 2–4
Sangamonian	*Eem or Ipswichian*	*Riss–Würm*	*0.095*	*MIS 5*
Illinoisan	Saal or Wolstonian	Riss	0.12	MIS 6
Yarmouthian	*Holstein or Hoxnian*	*Mindel–Riss*	*0.20, 0.31, 0.41*	*MIS 7–11*
Kansan III	Elster or Anglian	Mindel	0.44	MIS 12
Aftonian II	*Cromerian III–IV*	*Günz–Mindel*	*0.50, 0.60*	*MIS 13–15*
Kansan II	Cromerian B	Günz	0.65	MIS 16
Aftonian I	*Cromerian I–II*		*0.68*	*MS 17*
Kansan I	Bavelian/*Bavelian*		0.72–0.85	MS 18–21
Nebraskan	Menapian	Donau	0.87	MIS 22
	Waalian/Waalian		0.9–1.7	MIS 23–55
McGee	Eburonian		1.79–1.73	MIS 56–62
	Tiglian C		*2.06–1.83*	*MIS 63–77*
	Tiglian B		2.10, 2.18	MIS 78–82
	Tiglian A		*2.20–2.47*	*MIS 83–97*
	Pretiglian	Biber	2.48, 2.52	MIS 98, 100

proximity to the isotopically recorded cold peak at ca. 2.6 Ma (Table 1), which was responsible for the earliest known glacially derived sediments in Northern Europe (Head et al. 2008). But in addition, the IUGS also agreed to redefine the Lyellian Pleistocene by moving its GGSP from the base of the Calabrian Stage, where it had been located since 1948, to that of the Gelasian Stage, increasing its duration by some 44 %.

The action of IUGS was heavily criticized (i.e., Aubry et al. 2009), because the establishment of the new period flouted all basic guidelines of geochronology (Hedberg 1976; Salvador 1994). To begin with, it was framed in paleoclimatic terms and not in the context of marine paleontology, as for all other units in the time scale. In addition, it imposed a gross and undefended revision of the Lyellian Pleistocene in violation of the hierarchical logic of the GTS. Critics further pointed out that this ad hoc agreement to the preferences of the INQUA group disrupted half a century of literature in many other important areas of research, from marine paleontology to paleoanthropology, vertebrate paleontology, cyclostratigraphy, and paleoceanography, for whom the long-established and clearly dated Pliocene-Pleistocene boundary at Vrica, and not the concept of Quaternary climate, was a fundamental metric. Again, by imposing a new Period/System to replace the later Neogene without any justifying paleontological argument, the IUGS was seen to arbitrarily invalidate the Neogene (Hilgen et al. 2008). And finally, by casting aside Lyell's (1833) original biostratigraphic characterization of the Pleistocene that was embodied in the 1948 London recommendation, the IUGS casually destroyed the first and most historic GSSPs in the time scale.

In its consideration of the INQUA proposal, the ICS rejected counterproposals to make the Quaternary a Neogene subunit and did not consider other alternatives such as making it a separately defined "paleoenvironmental" sub-era of the Cenozoic on a par with Tertiary rather than Neogene or to restore the Pleistocene by inserting a new basal epoch (Hilgen et al. 2008; Aubry et al. 2009). The IUGS decision cannot be reopened for further discussion until 2019, at which time this long-enduring controversy may well be finally resolved (Table 1).

Quaternary Time Frame

The Milankovitch Cycles The unusual climatic conditions that distinguish the Quaternary were last seen over 300 million years ago, in the cyclothems of the Carboniferous. The advances and retreats of huge continental ice sheets in temperate latitudes are a response to cyclic variations in the Earth's orbit, which change the amount and location of solar radiation reaching the Earth's surface. Known as Milankovitch cycles after the Serbian geographer and mathematician Milutin Milankovitch, who first calculated them (see Imbrie and Imbrie 1979), these are caused by oscillations in the Earth's angle and in the shape of its orbit around the sun (Hays et al. 1976; Einsele et al. 1991).

Briefly, *precession* refers to the slow swing in the orientation of the axis every 22 kyr. Because the Earth's annual orbit is not precisely circular, at present, the winter solstice (i.e., when the North Pole points directly away from the Sun at midday) occurs when the Earth is closest to the Sun. This gives rise to warmer winters and cooler summers in the northern hemisphere and the opposite in the southern hemisphere. 11 kyr ago, it was the opposite, such that winters in the northern hemisphere were very cold, but summers were very warm.

The *obliquity* cycle refers to the rocking of the Earth's axis between 22° and 24.5° every 41 kyr, with minor frequencies of 29 and 54 kyr. This cycle has the greatest effect in high latitudes, because low obliquity means that there is less difference between summer and winter, and thus lowers melting rates of accumulated snow and ice.

Regular variations in the *ellipticity* of the Earth's oval orbit, under the influence of other planets, result in changes from nearly circular to more elliptical in cycles that repeat at irregular intervals concentrated around a 100-kyr frequency, as well as changes in the amplitude of the variation on a roughly 400-kyr period. Unlike the other two major cycles, ellipticity controls the total amount of solar radiation reaching the Earth's surface.

The overlapping cycles, each with their own frequency, reinforce or suppress each other's effects in evenly spaced harmonic "beats," recorded in a variety of proxies in the geological record (Berger et al. 1984; Burroughs 1992). Normally, the orbital cycles have relatively minor influence on world climate and are seen mainly in pulses of ocean productivity recorded as rhythmic bands of organic-rich layers, or *sapropels*, in deep-sea cores. The Cenozoic, however, is not a normal time, but one characterized by the rare condition of a major continent isolated under one of the poles (as with Gondwanaland in the Carboniferous, the last time the world experienced major glacial cycles). In these special circumstances, a great cap of ice will form that refrigerates the enclosing waters, which then sink into the depths and gradually fill the ocean basins from below. The effect of the Antarctic ice, which expanded to reach sea level some 38 million years ago, has changed the average temperature of the world's ocean (save for the thin sun-warmed film above the thermocline) from ca. 20 °C in the Eocene to ca. 4 °C today. Without the moderating influence of a warm ocean, continental climates in the higher latitudes have grown steadily more seasonal, and the Milankovitch cycles have had a steadily increasing influence.

In recent years, Milankovitch's calculations have been significantly extended and refined in computerized treatments that bring out the internal complexity of the orbital oscillations. Precisely because of this complex reality, the numerical values used in general discussions such as these are only convenient approximations. Furthermore, we need to keep in mind that each of the orbital variations differs from the others in its quality as well as its timing. The impact of astronomical forcing on Quaternary environments, as interpreted from the geological record, is reviewed in the following sections.

The "*Ice Ages*" Initially, with geological research confined to surface exposures on the land, only the broad effects of orbitally forced climatic cycles could be seen in the stratigraphy of continental and estuarine deposits adjacent to the continental ice sheets, where successions of tillite and loess, interspersed with region-wide erosional unconformities, were seen as evidence of the advances and retreats of continent-spanning ice, and Milankovitch's calculations remained largely speculative. The glacial histories were somewhat uncertainly correlated because the fossil record was not entirely adequate to distinguish one climax from the next and because the stratigraphy lacked consistent interregional detail. The more recent glacials could be more confidently identified around the world because the climatic swings had shifted to a new, more widely spaced and more pronounced rhythm (see below). These major peaks, as well as a few of the more notable pulses in the lower Quaternary, were the basis for the "glacial-interglacial" terminology of Quaternary paleoclimatists. More precise measurements have thoroughly exposed the inability of such conventional formulation to describe the climatically dominated history of the Quaternary, and the older "ice age" nomenclature is now seldom used. Even so, these terms, which identify the main features of the record, are still relevant to a complete picture of this time.

The difficulty of making out the precise details of Quaternary climate history in the prewar years was largely due to the nature of the data. The record on land, even taking into account the relative completeness of the record in North Sea estuaries (Zagwijn 1985), is still essentially discontinuous because of the episodic impact of thousands of cubic miles of ice moving on and off the continents, with major shifts in base level as world sea level rose and fell by hundreds of feet, together with the physical disruption of older sequences being plowed up by later ice sheets. For this reason the remains of a given "glacial stage" in most places on land represent but a small fraction of a glacial cycle, and much of the history of events during that time is not preserved. On the other hand, in the relatively undisturbed and uninterrupted deposition of fine annual layers in the deep ocean basins, the variations in environmentally controlled features can provide a virtually continuous record of long-term climatic change on a fine scale, and that can be compared on a worldwide basis.

Marine Isotopic Stages Soon after World War II, with new techniques in isotopic chemistry available as a side effect of the development of nuclear weapons, research began on whether long-term climate variations could be traced by changes in climate-dependant isotope ratios in seawater, as preserved in the calcium carbonate ($CaCO_3$) of marine shells. The research initially focused on the two stable isotopes of carbon, ^{12}C and ^{13}C, from piston cores in the Caribbean. The relative proportions of these isotopes vary directly with local water temperature, which required that sampling be limited to planktonic foraminifera from the upper few meters of the ocean, in order to maintain a constant environmental context. The results, however, were highly encouraging, showing a distinct periodicity at about 100,000 years (assuming a constant sedimentation rate), in clear synchrony with the Milankovitch calculations. These results justified the proposal, which was swiftly adopted by the profession, that marine isotopic stages, or MIS as they became known, could provide an improved calibration for the alternating glacial and interglacial cycles of the Quaternary (Emiliani 1955, 1966). From the beginning, the MIS were numbered so that the warm maxima – with the present interglacial as number 1– are odd and the cold peaks are even.

It was soon found that the ratio of the two most common isotopes of oxygen, ^{16}O and ^{18}O, exhibited a similar if not precisely coincident variation, also in the carbonates from deep-sea cores, but that the ratio was independent of local temperature and was instead constant in fossils from all paleodepths, indicating that the same oxygen isotope ratio characterized all ocean waters of a given time. On the other hand, the ratio of ^{18}O in freshwater is significantly lower than in seawater. Because the two isotopes differ strongly in mass, with ^{18}O some 13 % heavier than ^{16}O, water molecules with the lighter isotope evaporate at a distinctly higher rate than water with the heavier molecule and thus go preferentially into atmospheric water vapor, rain, and snow. Although ^{18}O is only 0.2 % of surface oxygen, the huge amounts of isotopically fractionated freshwater moving into ice sheets and back into the oceans during continental glacial cycles would result in measurable changes to the ratios in seawater. The oxygen isotope curve is then properly recognized as an ice-volume (i.e., sea level) curve rather than a paleotemperature curve (Shackleton 1967). Because the carbon isotope ratios are subject to uncontrolled sampling uncertainty, including unknown effects of postdepositional diagenesis and interaction with colder water at the seafloor, the oxygen isotope curve became the standard by which the effects of Milankovitch astronomical cycles were tracked in the Earth's climate history.

Using lengthy cores from DSDP (Deep Sea Drilling Project) sites in the Pacific, the oxygen isotope curve was subsequently extended into older levels (Shackleton and Opdyke 1976). Since the cycles in the deep-sea layers could not be directly dated, in the absence of unaltered volcanic debris, and because sedimentation rates are inherently irregular even in the least disturbed settings, the isotopic peaks were initially calibrated against the radiometrically dated boundaries of the paleomagnetic time scale. In a striking turnabout, however, the paleomagnetic boundaries themselves were subsequently redated in a new astronomical polarity time scale, or APTS, based on an improved version of Milankovitch's calculations, in which the mathematically determined age of orbital cycles was used to date the oxygen isotope peaks and thereby the associated paleomagnetic boundaries (Hilgen 1994). In the new calibration, the age of paleomagnetic reversals was slightly older, so that, for example, the Brunhes/Matuyama boundary went from 0.73 to 0.78 Ma, the top of the Olduvai went from 1.66 to 1.77 Ma, and the Gauss/Matuyama boundary went from 2.47 to 2.60 Ma (Berger and Loutre 1991; Hilgen 1994).

Whether the isotopic curve reflects global temperature indirectly or continental ice volume directly, it provides a clear story of changing and intensifying climatic swings over the span of the upper Pliocene and Quaternary. Aside from the stepwise increase in ^{18}O of seawater, which reflects the increase of permanent ice in the Antarctic ice cap, the most notable feature of the curve is the shift at MIS 22 from an obliquity-controlled frequency of ca. 41 kyr to an ellipticity-controlled frequency of approx. 100 kyr, with increased amplitude – i.e., greater volume of ice during more widely spaced glacial maxima. The first of these super maxima corresponds to the Menapian or Nebraskan at ca. 0.88 Ma and the beginning of the classic "ice ages" in the sense of Agassiz. The glacial-interglacial swings from this time to the present were still confusingly frequent to early stratigraphers, who often combined them, but their relation to orbital eccentricity signifies that the total amount of solar radiation reaching the Earth had become the controlling factor, rather than the variations of seasonality at high latitudes controlled by obliquity. In other words, that global cooling had reached a new low.

In pre-Menapian climatostratigraphy, two other distinct "ice age" glaciations were commonly identified, in maximum cold events that we now link to the roughly 410-kyr ellipticity amplitude beat. In the most thoroughly studied and most complete section exposed on land, in the Rhine delta of Belgium and the Netherlands, the glacial advance that corresponds to what is seen in the isotopic curve as the bifurcate maximum at MIS 60–62 (approx. 1.8 Ma) was termed the Eburonian. This event, which coincides with the cold-water deposits of the Calabrian Stage, was considered to be the opening episode of the Pleistocene until the IUGS moved the boundary. The other composite maximum of MIS 98–100 at approx. 2.5 Ma was identified as the Pretiglian glacial, a conspicuous event that climaxed the end of a significant downward step in climate, as the cyclicity shifted from precession-controlled, with a dominant frequency of 22 kyr, to the obliquity-controlled 41-kyr pattern of the next 1.6 million years (Lourens and Hilgen 1997). This was when the first continental ice sheet formed in Northern Europe and the first loess was deposited in northern China (Ding et al. 1997; Ehlers et al. 2011), justifying the current definition of the Quaternary and the relocation of the Pleistocene boundary to the base of the Gelasian Stage at 2.59 Ma. Shackleton et al. (1984) noted the presence of ice-rafted debris in North Sea cores slightly earlier in MIS 102, but this could have been due to mountain glaciers breaking off into the ancestral Rhine during this glacial maximum. The notable isotopic peaks at MIS 78 and 82, the strongest of pre-Menapian time, were in fact largely unrecognized in continental sequences aside from the North Sea, where this episode was seen as a glacial interlude in the extended Tiglian interglacial (Kuhlmann et al. 2006). The prolonged Waalian interval (MIS 25–55) was also generally considered to be an interglacial by the continental geologists, apparently because it was warmer overall than the Menapian and because its glacial maxima were relatively feeble in comparison with those of more recent times.

At the other end of the Quaternary time scale, the detailed history of the most recent glacial episodes, in which the history of *Homo sapiens* itself is involved, has been reconstructed back through four major glacial-interglacial cycles to about 420 kyr, according to variation in carbon dioxide and methane, and thus temperature, in lengthy cores taken from the stable ice caps of Greenland and Antarctica (e.g., Petit et al. 1999). Of particular interest is the termination of the final episode, the Weichsel or Wisconsin, whose great ice sheets in Eurasia and North America reduced sea level and exposed Beringia for the passage of humans into the New World, together with other still-enduring imprints on the fauna, flora, and topography of the higher latitudes.

At the present time, we live in one of the rare warm spells known as “true interglacials,” when the northern hemisphere ice sheets melt completely away from the lowlands surrounding the Arctic Ocean, leaving only the Greenland ice cap. The history of the next previous interglacial is instructive. This interglacial, identified as MIS 5e at 127 Ka, is the earliest of three subcycles in the brief warm interval prior to the Weichselian or Wisconsinan advance (Shackleton et al. 2003). During this maximum, identified as the Eemian or Sangamonian in continental stratigraphy, global sea level was several meters higher than at present – or, in other words, global warming, without any human intervention, was significantly greater than today. This would clearly suggest that our own interglacial is measurably colder than the previous one and that we are only at the beginning of the Ice Ages.

The record of the last glacial maximum – and, presumably, of the previous ones in the ellipticity-dominated later Quaternary – was punctuated by sudden melting episodes, known as Heinrich events after their discoverer (Heinrich 1988). These take the form of enormous catastrophic ice slides, equivalent to the sudden collapse of valley glaciers, or *jökellaups*, but of far greater scope, that covered the Atlantic in jostling armadas of gigantic icebergs and whose melting leaves distinctive layers of bouldery glacial debris across the ocean floor. The absence of normal planktonic microfauna in these deposits documents the presence of a relatively deep and long-lasting layer of freshwater that built up across the ocean as these masses of ice melted away over perhaps hundreds of years. This would have interrupted, or severely limited, the normal “conveyor belt” circulation that brings Gulf Stream warmth to the North Atlantic, suggesting that the Heinrich events created, rather than were created by, changes in ocean circulation (Broecker 1994; Sowers and Bender 1995). The relationship of Heinrich events to orbital forcing is not at all clear, given that the intervals between the last four events decreased from 13,000 to 7,000 years.

The ice core data have been interpreted (Sowers and Bender 1995) as evidence that concentrations of CO_2 and CH_3 began to rise, indicative of warming oceans, between 2,000 and 3,000 years before the final retreat of the ice caps.

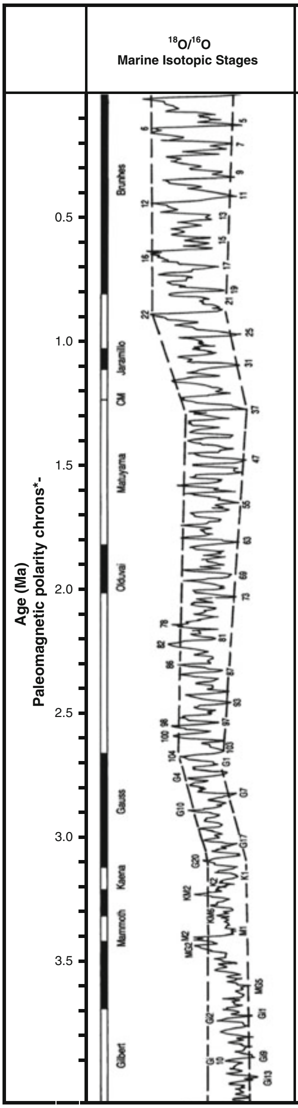
Quaternary Climate and Environments

As noted above, the cooling of the world ocean, augmented by mid- to late Cenozoic breakdown of equatorial circulation due to the northward movement of Africa, Australia, and South America across the formerly open midlatitude seaways, led to progressive steps of Quaternary climate deterioration at 2.5, 1.8, 0.9, and 0.4 Ma – i.e., Pretiglian, Eburonian, Menapian, and Elsterian glacial stages (Table 2). Each of these steps was more severe than the previous one, and each left an imprint on flora and fauna that was not erased in the subsequent warmer period. As a result, the world's biota became steadily more fragmented and impoverished, and weather patterns changed irrevocably into new patterns that had not been seen before.

Under natural conditions, just as with man-made pollution, the carbon dioxide content of the atmosphere plays a major, perhaps critical, role in controlling air temperatures and is the principal means by which orbitally driven insolation cycles influence climate. Solar radiation, in itself, does not heat the atmosphere. Instead, the energy in the visible and ultraviolet spectrum passes through, to be absorbed and reradiated from the Earth's surface in the infrared as heat energy. This recycled energy is emitted mainly from rocks and water and somewhat less from clouds and vegetation, which tend to reflect solar radiation back into space. Most of the reradiated heat is trapped in atmospheric water vapor, but carbon dioxide absorbs a great deal more per molecule. In this way, small changes in CO_2 can cause significant changes in the temperature of the atmosphere, with a strong secondary transfer of atmospheric heat back to the ocean surface.

The influence of CO_2 on temperature is itself dependent on temperature, in a crucial feedback loop only exhibited by this particular greenhouse gas. This comes from the fact that the amount of CO_2 in the atmosphere, setting aside the transient effects of vulcanism or drought, is fundamentally regulated by the process known as the "solubility pump," based on the changing solubility of CO_2 in ocean surface waters in opposition to changes in water temperature. As surface water warms, its ability to hold CO_2 decreases, leading to more CO_2 in the atmosphere and thereby even higher water temperatures and even more atmospheric CO_2, in a runaway escalation. On the other hand, the reflective properties of the Earth's surface, or albedo, affect the amount of radiant energy that is absorbed and reradiated as heat, so that a slight increase in reflective clouds and ice will decrease the heat energy available for CO_2. The declining atmospheric temperatures allow the oceans to

Table 2 Quaternary time scale. The ages of major Quaternary climate cycles in the North Sea record, as well as consensus land mammal terms, are given in the A(P)TS or astronomical (*polarity*) time scale and compared with climate cycles documented by oxygen isotope variations in deep-sea cores. Some significant localities and events applying to paleoanthropology are shown on the right



STAGE	GLACIAL *Interglacial*	Western Europe	Eastern Europe	Asia	North America.	Souh America	Africa	LOCALITIES	EVENTS
0.0117	WÜRM *Holocene* *Eem*	GALERIAN	TIRASPOLIAN	GONGWANGLINGAN	RLB	ENSENADIAN	NAIV	< Border Cave 0.075	
	RISS							< Laetoli Ngaloba 0.15	Modern Homo sapiens
							NATRONIAN	< Florisbad 0.26	
	Holstein				IRVINGTONIAN			< Kapthurin 0.35 < Swanscombe 0.4	
IONIAN	MINDEL								
	Cromerian III-IV								
	GÜNZ							< Bodo 0.64	"Archaic Homo sapiens"
	Cromerian i-II		TAMANIAN	NIHEWANIAN				< Atapuerca 0.78 < Zhoukoudian 0.78 < Elandsfontein 0.80	
	MENAPIAN	VILLAFRANCHIAN							First full glacial
0.96							TURKANAN	< Trinil 0.9	
CALABRIAN	*Waalian*		ODESSAN					< Barranca de León 1.4 < Olduvai Bed III 1.4	Homo in Europe
						UQUIAN		< Olduvai up. Bed II 1.6, <Sangiran 1.6 < Peninj 1.7	Homo in SE Asia
1.81	EBURONIAN		KHAPROVIAN		BLANCAN			< Swartkrans 1 1.80 < Dmanisi 1.81i	Homo in Eurasia
GELASIAN	*Tiglian C*			YOUHEIAN				< Langebaan up. 2.0 < Olduvai Bed 1 2.0	Earliest Homo fossils
	TIGLIAN B							< Sterkfontein 3 2.24	
	Tiglian A							< Loklalaei 2.34 < Hadar BKT-3 2.35 < Taung 2.45	
2.59	PRETIGLIAN					CHAPADMALALAN	AFARIAN	< Gona 2.53	Earliest stone tools
PIACENZIAN								< Sterkfontein 4 2.9	
			MOLDOVAN					< Makapansgat 3.2	
		RUSCINIAN						< Koro Toro 3.5	
3.60				JINGLEAN					
ZANCLEAN								< Laetoli (upp.) 3.85	

absorb more CO_2, lowering air temperatures even further and removing more CO_2, in a reversal of the self-reinforcing warming process. In this way, carbon dioxide acts to very significantly amplify the climatic effect of orbitally triggered variations in solar radiation.

Quaternary glacial episodes follow a very fixed pattern, beginning when orbitally forced lower winter temperatures result in increased winter precipitation (*pluvials* in the tropics) with deeper snow packs. With varying rates depending on reciprocal summer conditions, permanent ice cover will expand to cover ever wider areas, in a trend greatly augmented by reduction in atmospheric CO_2 and the growing size and persistence of polar air masses. At some point, however, the ice-covered area reflects so much solar radiation that global average temperatures reach a point where evaporation and thus precipitation is greatly reduced. The decline in cloud cover allows even more radiation to be reflected back into space, in yet another self-reinforcing feedback. This trend is augmented by the decline in rainfall outside of the glaciated area, which reduces vegetative cover and further increases reflectivity. Thus, all glacial-climate episodes of the later Cenozoic, whether mild or intense, normally begin with cool and wet conditions and climax with cold and dry; in higher latitudes, the climax is known as the *polar desert* phase. Because they "make their own climate," the cold, highly reflective continental ice sheets of the Northern Hemisphere tend to persist well past the climax phase and then catastrophically collapse during the early part of the interglacial interval. In much the same way, the climate and temperature trend leading to glacial maxima are relatively gradual compared to the sharp transition to interglacial conditions once the peak is reached. This asymmetry, as well as intensity, in Quaternary climate cycles is entirely due to the way the enhancing processes affect climate, in the absence of the smoothing influence of a warm ocean.

Adaptations of Quaternary Flora and Fauna The Quaternary glacial cycles had an enormous impact on the terrestrial biosphere, during the "full glacial" interval that began with the MIS 22 Menapian at 0.9 Ma, and not only in the higher latitudes. To choose a widely applicable and highly appropriate example, Grichuk (1997) itemized the sharp decline in diversity and range of the mid-Pliocene woody plant flora that was found across Eurasia, ranging from Italy and the Netherlands to central Russia and Siberia to southern China, over the course of the Quaternary. Of more than 70 genera that were present across the continent during the Pliocene warm climates prior to MIS G20, 60–75 % disappeared from their former regions in a progressive displacement or depauperizing that appears to have begun, in a mild way, in the latest pre-Quaternary, and which was essentially complete by the Menapian (MIS 22, 0.9 Ma). This displacement affected the less cold-tolerant majority of the paleoflora such as the contemporary species of walnut, cedar, hemlock, laurel, pomegranate, grape, and fig, among many others, leaving behind the modern forest assemblages that consist mainly or wholly of genera classed as panholarctic (pine, fir, willow, poplar, birch, etc.) and north temperate (oak, elm, beech, maple, linden, etc.), that persisted virtually unchanged through the remainder of the Quaternary.

A similar pattern of rapid pre-Menapian development of the "typical" Quaternary fauna of Eurasia was noted by Aguirre et al. (1997). To begin with, just as the Quaternary began, *Equus* and arvicolid rodents arrived from North America and *Mammuthus* from Africa – perhaps not unconnected to the Pretiglian sea level lowering – simultaneously with an overturn in the ruminant fauna. From this level up to the Menapian, the authors noted rapid evolution in small mammals and the last occurrence (extinction and/or emigration) of a number of Pliocene large mammal lineages including *Mastodon*, *Hipparion*, *Nyctereutes*, *Chasmaporthetes*, *Leptobos*, *Megalovis*, *Gazella*, and *Gazellospira*, coupled with the first appearance (evolution and/or immigration) of the modern genera *Canis*, *Panthera*, *Pachycrocuta*, *Hippopotamus*, *Bos*, *Bison*, *Dama*, *Capra*, *Ovis*, and *Cervus*, among others – not to mention *Homo*. As with the temperate forests, it seems clear that the Eurasian mammalian assemblages that developed in the early Quaternary were sufficiently well adapted to intensifying climate change that they could continue, with little further modification, after the beginning of the "full glacial" conditions at 0.9 Ma to the present day despite the greater stress imposed by these more extreme conditions.

Quaternary in Africa The relatively highly developed state of geochronometry and paleontology in Africa allows a detailed analysis of the effect of Quaternary climate cycles in the tropics, with direct application to human evolution. According to Trauth et al. (2007), the late Cenozoic climate of East Africa prior is characterized by brief, widely spaced intervals, during which the climate varies rapidly with short precession-driven cycles of extreme wetness and extreme aridity, which marked by expansion of Rift Valley lakes. Prior to 2.7 Ma, these unstable intervals occurred every 400 kyr in synchrony with the fundamental cycles of ellipticity amplitude, whereas during the Quaternary they occurred only three times on an 800-kyr frequency at 2.7–2.5 Ma, 1.9–1.7 Ma, and 1.1–0.9 Ma (perhaps a one–two beat in the amplitude variation?). These three major lake phases in the equatorial region are coincident with the three most significant transitions in the downward trend of global climates during the Quaternary: the onset of Northern Hemisphere glaciations during the Pretiglian stage, the intensification of the Walker Circulation in the Eburonian stage, and the mid-Pleistocene Revolution or "full glacial climates" in the Menapian stage, respectively. A fourth major event at ca. 0.2 Ma is not apparent, and it would seem that post-Menapian conditions may have moved to a new level in which phenomena typical of the early Quaternary are no longer expressed. The coincidence of rapid climate swings in the tropics with these major glacial advances is due to the stepwise compression of the Intertropical Convergence Zone, which made East Africa locally sensitive to precessional influence.

The influence of precession in the tropics is seen in the variation of precipitation during the summer monsoon in East Africa (Kingston et al. 2007). The monsoon, which was initiated by the onset of Walker Circulation in the Indian Ocean in early Quaternary time, has steadily intensified with continued cooling of the upwelling water, whose temperature contrast with warm surface water is essential to this wind pattern (Tuenter et al. 1993). The precipitation maxima during monsoons are more intensified and extend further northward during minimum precession and maximum obliquity. Precession also influences the seasonal timing of the occurrence of the maximum precipitation.

The cool climate peaks in the Quaternary appear to coincide with, and thus arguably to influence, both major events and also the adaptive directions in the cladogenesis of the Hominidae. In the *habitat theory* of Vrba et al. (1996), it is argued that paleoclimatic oscillations, with corresponding changes in vegetation, are correlated to pulses of faunal extinction and speciation. A basic assumption in this theory is that the fundamental adaptations of a taxon to specific vegetational habitats, which can become acquired and enhanced during the 100-kyr span of a single eccentricity-driven climate cycle, become more pronounced through natural selection and will thus be recognizable characteristics in the clades that emerge in this habitat. In this way, terrestrial mammal biomes may be characterized by a "vegetational physiognomy" that reflects the habitat of the ancestral population.

The most compelling, though still controversial, evidence for the relationship of climate change to human evolution is based on studies of the fossil evidence dated to or slightly before the crucial 2.5 Ma step in global cooling that marks the beginning of the Quaternary (Behrensmeyer et al. 1997). At approximately this time, biome boundaries, grading from dry grasslands through open woodlands to tropical forests, shifted markedly toward the Congo Basin, with the result that the grassland vegetation expanded at all latitudes, together with grassland-adapted mammals, including steppe inhabitants from the north such as *Equus* and *Oryx*. Supporting evidence for this shift comes from an increase of open-grassland pollen in both marine and terrestrial (particularly low-altitude basin) samples, although overall the regional environmental settings remained a mosaic of habitats.

The floral changes suggest a period of relatively xeric conditions and appear to correspond to a pulse of faunal extinctions and speciations in response to the relatively extensive and rapid environmental shifts. The selective pressures of this habitat change appear to have favored megadont adaptations for feeding on tougher, more fibrous fruit, leaves, and grass in the dry, open woodland-savanna environment. Among the megafauna, the bovids, suids, and elephantids with larger teeth and more robust jaws became more diverse and more abundant at this time, and this was also true for early hominines as well. In *Paranthropus robustus*, *Paranthropus boisei*, and *Homo rudolfensis*, all of which appear to have evolved ca. 2.5 Ma or soon after, the same tendency is seen to postcanine megadontia, heavily reinforced and massive facial skeletons supporting relatively large masticatory musculature and relatively thick enamel. In the retention of thick enamel, at least, modern humans exemplify Vrba's habitat theory and carry the signature of the grasslands where *Homo* first appeared, as the Quaternary opened the door for new specializations and opportunities.

Conclusions

The appearance of *Homo* just as climate changes became significantly more extreme with the beginning of the Quaternary cannot be a meaningless coincidence; the link would seem to be that both events are synchronous with the expansion of the grassland habitat of Africa, to which hominins were already adaptively committed. As the world continues to cool with no end in sight, the increasingly stressful impact of orbital cycles on the planetary environment may also be linked to the increasingly resourceful adaptations of the hominin lineage. In fact, if we accept that natural selection is driven primarily by environmental change, we cannot avoid a very strange and simple conclusion: that the breakthrough into sentience that makes us able to read and write these words about the Quaternary would not exist, but for the existence of the Quaternary itself.

Cross-References

- ▶ Chronometric Methods in Paleoanthropology
- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Overview of Paleolithic Archaeology
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Quaternary Deposits and Paleosites
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments

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Quaternary Deposits and Paleosites

Klaus-Dieter Jäger

Contents

Abstract

Due to the mineral content of bones and teeth, the majority of fossil hominid remains are represented by these tissues; soft parts of the human body are preserved only very rarely. Whether or not fossils are well preserved depends not only on their own composition but also on the nature of the deposits that enclose them, which as a rule are sediments of the Pliocene, Pleistocene, or Holocene age. Numerous methods are now available for chronometric dating of hominid fossils, though none of them is applicable in all situations. However, it is still necessary to situate each hominid fossil within the larger stratigraphic framework. Hominid evolution began well over 4 million years ago and continued through the final part of the Neogene (Upper Tertiary). As a result, ongoing international discussions of stratigraphic boundaries over this time span are significant for the assessment of hominid evolution. In addition to providing

K.-D. Jäger (✉)
Institut für Prähistorische Archäologie, Martin Luther-Universität Halle, Halle, Germany
e-mail: speler@praehist.uni-halle.de

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stratigraphic information, paleoanthropological sites offer insights not only into the environmental background of the fossils they yield, but in later periods commonly also into the cultural evolution of mankind and its relatives.

Introduction

The Tertiary-Quaternary boundary lies between the Pliocene and Pleistocene epochs. Due to the fact that the terms Tertiary (resp. "*tertiaire*") and Quaternary (resp. "*quaternaire*") were proposed in the early nineteenth century (for the scientific history of this question see Van Couvering, this volume) there is ongoing debate on the proper definition and even the usefulness of both terms (Cepek and Jäger 1988; Gradstein et al. 2004; Jäger and Ložek 2003, 2005; Pillans 2004). While in the past the most frequently accepted timing of the T-Q-boundary was around 1.8 Myr ago, with the beginning of the Calabrian Stage, in 2009 the International Union of Geological Sciences (IUGS) redefined it at the base of the Gelasian Stage, approximately coincident with the isotopic cold peak that occurred at about 2.6 Myr.

The Quaternary, consisting of the Pleistocene and Holocene epochs, is a comparatively short geological period, characterized by a series of significant long- and short-term climatic fluctuations, by the origin and expansion of the genus *Homo*, and finally by the rise of anatomically-modern *Homo sapiens*. Since the Quaternary paleoenvironmental background is essential for fleshing out the evolution of our genus, this contribution focuses on the following seven aspects, in turn: (1) the characteristics of fossil remains; (2) the characteristics of fossiliferous deposits; (3) possible methods for dating; (4) geochronometric perspectives; (5) global stratigraphic contexts; (6) environmental dependencies of paleosites; and (7) archaeological context.

Characteristics of Fossil Remains

Among preserved human remains, hard components from the skeleton, i.e., bones and teeth, are more commonly found, whereas soft parts are rare. The preservation of bones and teeth is determined by the content of calcium carbonate in the fossiliferous deposits. In the case of soft parts, their accessibility to decomposition is determined by the contemporaneous availability of water and atmospheric oxygen. If one of these two factors is kept to a minimum, the decomposition processes slow down or cease.

The availability of atmospheric oxygen is reduced in the case of subaquatic sedimentation or sediment conservation (e.g., in inland waters) or in the case of deposits lying below the groundwater table (e.g., peat in boggy terrain). Such conditions characterize the sites of bog bodies. On the other hand, desert areas with minimal water supply provide plenty of access to atmospheric oxygen, but the decomposition of organic matter is impeded by the lack of water. In these areas, an essential precondition for a lot of chemical processes is missing. Consequently, under such conditions the decomposition of organic matter is reduced. Instead, deserts frequently offer the prerequisites for mummification.

More often the preservation of fossil remains is restricted to hard components only. Independent of the local presence of water and atmospheric oxygen, the preservability of bones and teeth is a function of their apatite content, characterized by the formula $3Ca_3(PO_4)_2 \times CaF_2$.

Fossils in limeless deposits are protected from progressive corrosion and destruction since the superficial precipitation is not pure water.

As rainwater passes through the atmosphere prior to precipitation, it is contaminated by carbon dioxide (CO_2). Consequently, a weak carbonic acid (H_2CO_3) touches every surface, and the lime content in the soil comes in contact with the acid according to the following formula:

$$CaCO_3 + H_2O + CO_2 \rightarrow Ca(HCO_3)_2$$

If the subsoil contains a lot of calcium carbonate or a diffuse lime distribution, the first stages of decalcification are concentrated on the lime content of fossiliferous deposits and buried soils, and for a while bones and teeth remain protected against corrosion and dissolution. In limeless deposits, by contrast, such fossils are the only objects vulnerable to corrosive processes.

Characteristics of Fossiliferous Deposits

At more advanced stages of decalcification, even bones and teeth in limy deposits are exposed to corrosive destruction, but to a lesser degree. It is more or less insignificant whether the fossiliferous sediments in such limy deposits are loose ones with high porosity (such as sands or loess) or solid rocks (like travertine). Both provide sufficient and favorable conditions for the preservation of human skeletal remains, and this is why finds and sites of paleoanthropological significance are mainly connected with such deposits. Specifically, favorable conditions are shared mainly by the following sediment types:

1. Fresh-water lime deposits (calcareous deposits from inland waters, as a rule consisting of >90 % $CaCO_3$, frequently modified by diagenesis and found especially in travertines)
2. Loess (dust deposits of eolian origin, characterized by lime content usually ranging between 15 % and 30 % $CaCO_3$) with dust layers, intercalated by buried soils, frequently with calcareous (and also with decalcified) humus horizons
3. Cave deposits, especially in karstified calcareous mountainous regions, where caves originated from subterranean drainage ways and were subject to human entry and settlement after drying (which often happened after rerouting of the original waterway)

4. Calcareous debris, especially in mountainous regions, in open-air sites (with the lime content of the rock detritus being identical to that of the solid rock, perhaps less in the intermediate matter)
5. Calcareous fluvial and deltaic gravels and sands (although these more commonly contain displaced objects)
6. Calcareous lacustrine and beach deposits, as a rule silty and clayey, sometimes laminated

In addition to these site types, those favoring the preservation of soft parts (as in the case of bog bodies) have to be considered; these typically consist of peat and limnic mud layers.

Finally, tephras, i.e., pyroclastic deposits traced back to nearby volcanic eruptions—as in the case of Vesuvius during August of AD 79—enable the origination and preservation of human body imprints, which can be replenished by means of gypsum after detection. The method for such a procedure has been applied since the 1860s (since the year 1863, to be precise), first of all by the Italian archaeologist Giuseppe Fiorelli. Fiorelli was the long-standing leader of the excavations at the ancient town Pompeii, which was covered by tephra and pumice on the occasion of the AD 79 Vesuvian eruption (Mau 1899). Exceptional finds of this type are, e.g., the brain endocasts from the Eemian travertine at Gánovce in Slovakia (Vlček 1955, 1958).

Possible Methods for Dating

In many places, the geological preconditions for fossilized human remains coincide with sites of archaeological discoveries proving previous human presence or even settlement. That is why it is frequently the case that sites of significant paleoanthropological finds are also highly important in terms of archaeology. Not least, such in-site combinations facilitate the dating and the cultural-historical assignation of the respective paleoanthropological observations.

Moreover, the calcareous deposits mentioned above enable not only the preservation of human skeletal remains but also of comparable animal records. Both the paleozoological investigation of skeletal parts, yielding evidence for the early presence of micro- and macromammals, and the determination and examination of fossil shells, providing evidence of former molluscs or ostracods, contribute to biostratigraphic datings and paleoecological assessments. The investigation of mollusc remains is of special validity in central and western Europe, since precise species determinations have been achieved in these regions based merely on conchylia or even just their fragments (Ložek 1955, 1964). Comparable methods of dating are also in preparation in other parts of Eurasia (Meng 2003). However, investigations of micromammals as well as of molluscs are not restricted to qualitative records. On the contrary, both categories of fossils provide opportunities for quantitative analysis and statistical consolidation of results. Moreover, their examination permits the reconstruction of faunal assemblages as a basis for paleoecological interpretation (Rousseau 1990). They thus contribute to the characterization of the natural environment surrounding previous human populations.

In travertines, the paleozoological record is often complemented by leaf imprints and incrustations of various plant structures, contributing both to the dating of sites and to their paleoecological characterization. In sequences of peat and limnic layers of mud or marl, pollen analysis frequently offers an adequate method for dating. Thus, paleobotany as well supports the dating of fossil human remains as well as the reconstruction of the paleoenvironment, especially in the case of travertine and bog sites.

However, all of these paleontological and archaeological procedures and observations contribute only to the *relative chronology* of sites (see chapter "▶ Chronometric Methods in Paleoanthropology," Vol. 1), whereas the establishment of an absolute chronology—or "*calendar chronology*"—covering the whole time span of fossil hominids requires another methodology.[1] The calendar chronology of fossil hominids is based mainly on physical procedures, as summarized by Geyh (1980, 1983) and Wagner (1995, 1998), among others (see chapter "▶ Chronometric Methods in Paleoanthropology," Vol. 1). The preferred methods are radiometry (based on ^{14}C, uranium series, $^{40}K/^{40}Ar$, and others) and luminescence procedures (TL, OSL, IR-RF). The last 10–12 Ka is also within the reach of the botanical method of dendrochronology, but in practical terms this method is restricted to wooden objects. Consequently, paleoanthropological finds can only be dated by means of dendrochronology when they are associated with preserved wood. In central Europe, the range of oak chronology provides "a high-resolution time scale for nearly the last 12,000 years" (Spurk et al. 1998, p. 1114). However, the preservation of wood is, as a rule, subject to the same prerequisites as mentioned above with regard to soft parts of human bodies.

Geochronometric Perspective

The choice among procedures that are suitable for the numerical dating and calendar chronology of finds proving the presence of fossil men or early hominids is influenced to a high degree by the characteristics of the surrounding fossiliferous deposits. Different compositions of preserved material require the application of different methods. It follows that there will be differences in precision and range of dating. As a general rule, a short range is the inevitable consequence of precise temporal resolution and vice versa. Consequently, and independent of the datable material, the older the finds are, the more imprecise the numerical dating will be.

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[1] A note on terminology: As a rule, the search for more or less precise dates, both in the geosciences and in archaeological disciplines, is focused on so-called "absolute" chronology. However, already during the early 1980s, the paleontologist Jaeger (1981) claimed that this term is erroneous and – strictly speaking – inadmissible, since it assumes the existence of absolute time, which is physically and philosophically impossible.

The trade-off is comparable to the situation in optics, where the perceptibility of objects decreases with increasing distance. But this is only one aspect of geochronometry.

Another aspect relates to the dated material. Fossil remains of men from historical times and, going back further, from the last millennia can frequently be dated directly, e.g., by using the radiocarbon method. In contrast, fossil remains from the Middle Pleistocene – that is, finds that are several hundreds of thousands of years old – are not datable directly; however, as a rule the enclosing fossiliferous deposits may be subjected to numerical dating, e.g., by means of uranium series in the case of travertine deposits or by application of luminescence procedures in the case of loessic deposits. A larger age characterizes the early stages of hominid evolution, as evidenced by the occurrence of australopithecines. Such discoveries can be dated with only a few methods, e.g., the potassium-argon method (^{40}K/^{40}Ar); as a result, only rocks and loose deposits of volcanic origin can be analyzed. This has the useful application, however, that layers of lava rocks and tephras can be dated at sites of fossil hominid remains, if such layers are included in the stratigraphic sequence. In these cases, then, the materials subjected to dating are not the fossiliferous deposits themselves, but distinct layers in the sequence that includes the fossiliferous deposits. Consequently, the chronological investigation is restricted to time-marks in the local stratigraphy of the research site (cp., e.g., Fitch and Miller 1976; Ullrich 1983, Fig. 3).

Global Stratigraphic Context

Hominid evolution started more than 4 Myr ago (cp Johanson and Blake 1996, p. 23). As mentioned in the Introduction, according to resolutions of the IUGS on the occasion of international congress meetings (London 1948, Moscow 1984), this time span was subdivided by the boundary between two different geological systems, i.e., the Tertiary and the Quaternary (see chapter "▶ Quaternary Geology and Paleoenvironments," Vol. 1) (Aguirre and Pasini 1985; Partridge 1997; for background on the history of this decision, see Cepek and Jäger 1988). The chronological position of the boundary was set down at 1.64 or 1.8 Ma. The Tertiary and Quaternary systems share the common feature of significant long-term climate fluctuations, but are nevertheless noticeably distinguished by the average magnitude of the temperature oscillations around their mean values, especially in middle and higher latitudes of the globe.

Recently, the International Commission on Stratigraphy (ICS), a body of the IUGS with the authority to make recommendations related to a worldwide geological timescale, has presented a proposal aimed at the removal of this stratigraphic boundary by extending the preceding system of the Neogene, i.e., the Upper Tertiary, to the present (Gradstein et al. 2004). However, there are serious objections to this proposal (Claque et al. 2004), in light of the fundamental environmental changes during the relevant period (Gibbard 2004; Pillans 2004; Van Couvering 1997).

Independent of these ongoing discussions, the actual fixation of the debated global stratigraphic boundary at 1.64 or 1.8 Ma seems an unfortunate decision (Cepek and Jäger 1988). The chronological base of the younger system or period might be defined more properly at 2.6 Ma (Gelasian stage of the Pliocene series of the Neogene to date; Pillans 2004).

Environmental Dependencies of Paleosites

Climatic fluctuations over several hundreds of thousands of years, as mentioned above, not only determined the environmental conditions for previous hominids both in the temperate zones and in polar and subpolar regions, but also influenced human site selection and the chances of fossil preservation. Varying climate conditions favored different processes of sedimentation and, consequently, different types of deposits.

Thus, during prolonged cold periods, i.e., the glacials, the advance of glaciers in subpolar and mountainous regions was accompanied by periglacial and climatically continental circumstances in lowlands and hilly uplands of midlatitudes, which favored eolian deposition, mainly of dust. Consequently, hominid finds from glacial periods have frequently been made in loess sequences, as for instance at Dolní Věstonice in the Czech Republic and at Austrian sites.

On the other hand, many sedimentation processes can take place under warm—frequently under warm and wet—environmental conditions only. The respective deposits could originate either under a constant warm climate, as in the tropics, in lower latitudes, or in the warm phases of glacial cycles, the so-called interglacials, in the midlatitudes. This is why the interglacials favored such deposits as travertine and peat. Travertines may be defined as consolidated freshwater lime deposits, especially calcareous tufas.

As mentioned above, especially the travertines have provided excellent conditions for the preservation of finds, as well as for environment reconstruction. Moreover, the origination of these deposits required the proximity of springs and water, due to the dependence of all freshwater lime deposits on hard water. Owing to the significance of water for human life, sites of travertine formation were also frequently preferred locations of human presence and settlement. Consequently, man has often visited such sites and his remains can be discovered there frequently. Examples in central Europe are the well-known interglacial sites at Gánovce, Tata, Taubach, Stuttgart-Bad Cannstatt, Weimar-Ehringsdorf, Bilzingsleben, and Vértesszölös. Due to human presence and activities at such sites, they are significant not only when seen from a paleoanthropological angle but also as a result of archaeological discoveries.

As a rule, interglacial deposits, such as peat, mud, or travertine, contain assemblages of floral and faunal fossils and thus provide opportunities for quantitative paleontological analyses. Differences in age are reflected in differences in assemblage composition recorded by pollen, conchylia, or micromammal bones and teeth. Consequently, suitable methods of quantitative paleontological analysis aimed at biostratigraphic indications and correlations are pollen analysis (peat, mud), paleomalacology, and the investigation of micromammal remains (especially in travertines).

When differences related to the composition of the flora and fauna which accompany fossil hominid remains are taken into account, a relative chronology of sites can be developed based on biostratigraphy.

This approach is exemplified by the application of paleomalacology to famous interglacial travertine sites in central Europe (Jäger and Ložek 2003), including significant places of paleoanthropological discoveries (Jäger and Ložek 2005). Sometimes biostratigraphic indications lead to revision of previous chronological assignations of particular sites. This was the case, e.g., at Weimar-Ehringsdorf in Thuringia, Germany (Jäger 2001; cp also Mania 1993; Steiner 1993). Such corrections may help clear up seeming discrepancies in the paleoanthropological record. At Weimar-Ehringsdorf the original stratigraphic assignation to the Eemian (last interglacial of the Pleistocene) seemed to recommend a classification of the finds within the realm of the Neanderthals, whereas their later examination by Emanuel Vlček (Prague) emphasized similarities of the cranium (e.g., the occiput) to stratigraphically earlier crania at Steinheim (Baden-Wurttemberg, Germany) and Swanscombe (UK) (see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3). As chronometric datings of the accompanying fauna and flora by Mallik et al. (2000) have confirmed, the stratigraphically determined age and the osteological record of the human remains are now in line.

Archaeological Context

The majority of the sites providing fossil human remains, both from early hominids and from modern humans, have enabled archaeological observations. To be precise, at many sites bones and teeth prove the previous presence of human beings, while at the same time accompanying archaeological finds or man-made modifications of the site tell us about human activities, behavior, and lifestyle. This is why frequently at sites of paleoanthropological significance, archaeological discoveries are made as well. This is true both with respect to early hominids like Koobi Fora (in the Turkana Basin, Kenya: Coppens et al. 1976) or Hadas (Awash region, Ethiopia: Kimbel et al. 1982) and with respect to later humans (see chapters "▶ The Species and Diversity of Australopiths," and "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3).

Since the Middle Paleolithic, a considerable share of the available evidence has come from burials. This dating means that even Neanderthals are among the number of specimens recorded in this way (cp. the summarizing survey by Bosinski 1985, pp. 44–52). In this context one might mention, for example, the famous specimens at Le Moustier and La Chapelle aux Saints in France, or the "Old Man" from the Shanidar cave in Iraq (see chapters "▶ Neanderthals and Their Contemporaries," and "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3).

During the Upper Paleolithic, the number of burials increased (see chapters "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," and "▶ Neanderthals and Their Contemporaries," Vol. 3). Among the finds from this era is a female individual from the Pavlovian site at Dolní Věstonice (Moravia, Czech Republic) who was portrayed in a contemporaneous ivory carving from the same site (Klima 1983, pp. 83–89). During the Holocene, comprising the last 11,600 years (Litt et al. 2001), *Homo sapiens* is represented not only by single burials but rather by multi-individual cemeteries of different age, occasionally comprising hundreds of burials or more (e.g., Hallstatt in Austria, Early Iron Age, mainly eighth to sixth century BC, where ca. 1,300 burials going forward all the way to the twentieth century AD have been discovered: Kromer 1959; Sacken 1868; later Pauli 1975).

Burials favor the preservation of bones and teeth jointly, frequently even in the original articulation (see chapter "▶ Taphonomic and Diagenetic Processes," Vol. 1). Burials aside, the previous presence of humans at a site of discovery can often be proved for other reasons. Thus the preselection of sites of later—or current—evidence of habitation for paleontological investigations could involve a sleeping site in the case of early hominids (see chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 3), as exemplified by the cave system of Swartkrans in Southern Africa (with finds of *Paranthropus*, according to Brain 1983). In later periods, humans frequently used the sites of record for settlement as well as for activities of everyday life, art, and other cultural purposes. Well-known examples have been recovered in caves as well on open ground.

An outstanding example of cave occupation by previous residents is given by site 1 at Chou Kou Tien (Zhoukoudian) near the Chinese capital Beijing (Peking), well known as the eponymous site of the so-called Peking Man (*Sinanthropus* respectively *Homo erectus pekinensis*; chapters "▶ Later Middle Pleistocene *Homo*," and "▶ Defining *Homo erectus*," Vol. 3; Wei 1988; Huang 1998; Brühl and Laurat 2000, pp. 9–10 and pp. 94–100). Evidence of Neanderthal men found in these caves has proved that these locations were both residential and burial sites. The former are usually distinguished from the latter by the irregular scattering of more or less isolated bones and teeth.

The same feature of co-occurrence of paleontological and archaeological finds characterizes residential sites on open ground. However, if calcareous deposits are present in the subsoil to some extent, then such archaeological sites also favor the preservation of bones and teeth and, more frequently, of isolated and often fragmentary objects.

In situ preservation of the original depositional conditions is provided especially at travertine sites (e.g., Vértesszölös in Hungary: Kretzoi and Dobosi 1990; Bilzingsleben in Germany: recently Mania 1999; Weimar-Ehringsdorf, likewise in Germany: comprising Steiner 1981; Vlček 1993) and at loess sections (e.g., Dolní Věstonice in Moravia, Czech Republic: Klima 1983; Vlček 1991; chapters "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," and

"▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," Vol. 3).

Fluvial and deltaic as well as—rarely—marine deposits as a rule contain not only isolated and more or less fragmentary parts of the human skeleton, but also dislocated parts. Well-known examples are the famous early mandibles from Dmanisi in Georgia (Bosinski 1995; chapters "▶ *Homo ergaster* and Its Contemporaries," and "▶ Defining *Homo erectus*," Vol. 3; Dzaparidze et al. 1992; summary by Justus et al. 2000; Lordkipanidze et al. 2013; Sander 2013) and from Mauer near Heidelberg in Germany (recent discussion of the local situation: Fezer 1992; Zöller and Stremme 1992; Löscher 1996; von Koenigswald 1996; Wagner et al. 2007), as well as the cranium found at Steinheim/Murr in southwestern Germany (Adam 1988).

By contrast, in the case of bog bodies preservation has frequently taken place not only of the original articulation of bones and teeth but also of soft parts of the human body (see a.o. Hahne 1918; Dieck 1965; Glob 1969; Brothwell 1986; Turner and Scaife 1995; Gebühr 2002).

Conclusion

Depending on the composition of fossil human remains (mainly bones and teeth), their preservation as a rule is associated with certain sediments— mainly calcareous ones—from either the late Neogene (Pliocene) or, quite often, the Quaternary (Pleistocene and Holocene). The stratigraphic position of these fossils within the realm of the Quaternary or Neogene enables chronological arrangement of the finds, with increasing precision towards the present. Remains of fossil flora and fauna provide additional insights into the environment and circumstances of life of past human beings. Frequently, the detection and discovery of fossil remains has been favored by archaeological excavations and investigations of former settlement and burial sites.

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Paleoecology: An Adequate Window on the Past?

Thorolf Hardt, Peter R. Menke, and Britta Hardt

Contents

T. Hardt (✉)
Museum, Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany
e-mail: thorolf.hardt@senckenberg.de

P.R. Menke • B. Hardt
Institut für Anthropologie (1050), Johannes Gutenberg-Universität Mainz, Mainz, Germany
e-mail: pmenke@gmx.de; brittahardt@gmx.de

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Abstract

Starting from Ernst Haeckel's famous definition of ecology, our review considers the premises and the meaning of paleoecological research. Unlike current ecology, paleoecology has to pay more attention when dealing with "real" reconstructions. The concept of uniformitarianism is presented and demonstrates the importance of philosophical constructs in scientific work. Middle-range theory attempts to filter out false conclusions. Abiotic factors have had a strong influence on adaptive evolution; volcanism, tectonics, and climate exemplify this. Subsequently, we address biotic aspects of fossil findings, and in this context we discuss taphonomy, stratigraphic research, and interactions between floral and faunal environment. In a synthesis, we present three cross sections of human evolution at different time horizons (early-middle-late) to exemplify the inevitable multidisciplinarity of paleoecology, and we present some key events that probably altered the direction of radiations among hominids. Obviously, human evolution is not a special kind of evolution; it follows the rules of evolutionary biology, and hence depends undoubtedly on environmental influences.

Introducing (Paleo)ecology

In a strict sense, paleoecologists try to detect all processes which have affected a fossil organism *antemortem* (Behrensmeyer 1992). *Postmortem* events are analyzed by the methods of taphonomy and by studying diagenesis (Andrews 1992; Lyman 1996). One has to realize that these two fields are inseparably linked when dealing with fossils and the reconstruction of their environments. Here is illustrated briefly what (paleo) ecology is, followed by a discussion of actualism (or uniformitarianism) as an essential aspect of paleoecology.

Neoecology Versus Paleoecology?

Haeckel (1866, p. 286), who introduced the term "ecology" (German, Oecologie; nowadays, Ökologie) stated:

"Ecology is a part of science that deals with the relationships between organisms and their surrounding environment, wherein we can place all conditions of being in the broadest sense. These are of partly organic, partly inorganic nature; and both are of utmost importance for the form of organisms, because they force it to adapt to them" (translated and shortened by the authors).

Haeckel included the following aspects in his "conditions of being":

1. Abiotic factors (physical, chemical, climatic, electricity conditions; inorganic food; composition of water and soil)
2. Biotic factors (all relationships between organisms)

More recently, modern ecology has been defined as "the study of the relations between organisms and the totality of the physical and biological factors affecting them or influenced by them" (Pianka 1983, p. 3). Among its most interesting branches are the distribution and frequency of organisms/populations/communities, hence natality, mortality, and migration (Begon et al. 1998). It makes sense to divide ecological research into three subsections (Table 1).

All of these definitions are crucial when talking about ecology; however, for several reasons, it is not that easy to simply insert the prefix "paleo" for the study of ancient ecologies (Andrews 1992; Rull 2010).

There are not only strong connections between paleoecology and recent (neo, contemporary) ecology (sensu Rull 2010) but also some basic differences (Table 2). In spite of these differences, Rull (2010, p. 1) claims that "...ecology and paleoecology are only different approaches with a common objective, which is the ecological understanding of the biosphere. [...] It is recommended that ecologists and palaeoecologists develop joint projects," and further on "... a palaeoecologist is not simply a palaeoscientist whose data may be of interest for ecology but is primarily an ecologist working on another time scale, with different methods."

Table 1 Subsections of ecological research: (1) autecology that aims at all aspects of an individual as representative of its species and intraspecific questions, respectively; (2) demecology that deals with the interactions of a certain population with its environment; and (3) synecology that refers to all questions of interspecific relationships within an ecosystem

	Reference object	Reference parameter
Autecology	Single organism	Environment
Demecology	Homotypical community of organisms (population)	Contemporaries and environment
Synecology	Heterotypical community of organisms	Contemporaries and environment

Translated according to Schwerdtfeger (1968) and Tischler (1993)

Table 2 The differences between contemporary ecology or neoecology and paleoecology

Contemporary ecology or neoecology	Paleoecology
Source: currently living organisms in an intact ecosystem	*Source*: fossil assemblages and age estimation data
Precise and comprehensive description of environments and organisms in an ecosystem, parameters can actually be measured	Mostly characterization of a former milieu in order to subsequently state inferences on environmental and organismic factors
Potentially all faunal and floral components are available in the observed biocenosis	Fossils are the only documents available; hardly ever is the fossil record complete and many questions remain unanswered
Data acquisition is limited to a few years or even months/days	Excavated facies span a time of thousands and even millions of years

Compiled and extended from Etter (1994)

Paleoecological research is aimed mainly at analyzing long-term trends because when dealing with fossils, short-term processes (e.g., successions, microevolution) are not recognizable, or recognizable only with difficulty. Frequently, paleoecological analyses focus on the development of communities, in particular paleoenvironments, over time spans of millions of years (Stanley 1994; de Menocal and Bloemendal 1995). Or they combine the fossil record with molecular phylogenetics focusing on diversification patterns and speciation requirements (Benton and Emerson 2007). Despite the fact that there is a conspicuous nexus between organismic paleoecology and geologically orientated facies observations, it is preferable in practice to separate the two, since both disciplines are in themselves multilayered and sophisticated networks (Etter 1994; Seppä 2009; Sahney et al. 2010). Contemporary paleoecological questions include:

- Are similar as well as different morphological characters linked to adaptations in the same kind of habitat?
- Are there interdependencies between paleomilieu and life cycles/life-history parameters/population densities?
- How is distribution and diversity of life on Earth dependent on ecological requirements – especially biome shifts and ecosystem development (Sahney et al. 2010)?
- How do these transformations interact to species adaptation/migration and population changes?
- Can extinction and even speciation events be traced back to major changes in the environmental conditions, and if so, to which?
- What are the rates of speciation and extinction?

All of these questions require a high degree of multidisciplinarity and cannot be solved only in terms of single-factor analyses (Seppä 2009). They also have to encompass multiple factors that build ecosystems like the one covering our planet.

After a short look at the approach of actualism/uniformitarianism, we will take the previous quotation by Haeckel as a guidepost for the following sections. After touching on abiotic factors, we proceed to the biotic ones and finally merge them in a third step that we designate as synthesis. In the latter we try to focus on hominid or near-hominid evolutionary perspectives and ignore, because of solely talking about terrestrial systems, important paleoecological aspects that refer to marine ecosystems.

"The Present Is a Key to the Past": A Valid Premise?

One of the most important concepts in the geosciences is *uniformitarianism*, a principle introduced by the Scottish physician and geologist James Hutton (1726–1797). Originally, this was framed as an antithesis to the idea that catastrophic phenomena might have formed the Earth's surface. It was the establishment of the idea that the laws of nature stay constant that made geology a mature part of the scientific endeavor. This philosophical approach is axiomatic in physics, but it was Sir Charles Lyell, "Darwin's guru and intellectual father figure"

(Gould 1994, p. 6764), who placed this idea before a broader scientific community. The application of this principle inspired Darwin, although Gould (1994) warned against the pure extrapolationism of Darwin's uniformitarian perspective. Gould's (1994, p. 6768) attractive musings on paleontology's meaning are more important than ever. The simplemindedness of universal reduction to lower levels must be abandoned: "Our evolutionary world is a hierarchy of levels, each of legitimacy and irreducible worth." Riedl (1981) also emphasized the limitations of each methodological level.

Based on Gould (1984); Etter (1994) reduced the philosophy of actualism to four principles:

1. Laws of nature do not change on Earth in time and space.
2. Processes that influenced geological phenomena in the past occur in the same manner now.
3. The speed of geological and biological processes does not change.
4. In the past the same materials and the same conditions existed.

The first two of these are methodological assumptions that are necessary to conduct inductivist research. Points three and four are less definite. As Etter (1994) points out, the adoption of all four premises may be limited due to (1) constraints of observing the past and (2) the strong fluctuations of geological phenomena which occurred long ago (e.g., the circumstances of the dinosaurs' extinction). Even if the core of uniformitarianism is still valid, today's researchers expand their view, monitoring large-scale systemic processes or patterns that may explain what we are really able to learn about the guidelines in the continuum past-present and how we are able to adopt the results for future predictions (Dearing et al. 2006; Rull 2010). Although the mass of available data increases drastically, we should not forget to use the fossil record as a "litmus paper" to adequately evaluate the results (Jackson and Erwin 2006).

Dodd and Stanton's (1990) taxonomic uniformitarianism is a derivative of substantive uniformitarianism and an attempt to reconstruct ecological niches by assuming that the environment of a fossil will have been identical with that of the nearest extant relative. But it is obvious that reliable conclusions can only be made in this way if a fossil is a member of an extant species. This can virtually never be the case except for Pleistocene and Holocene deposits (Etter 1994), and even then there are also theoretical problems, one of which is the fragmentary knowledge researchers have of former ecological niches. An absence of enemies could, for example, have caused an expansion of the niche. Thus Etter (1994) admits that taxonomic uniformitarianism should be limited to fossils with extant representatives or relatives. Yet the method can be improved by investigating groups of species within a taxonomic group rather than just one.

Tattersall (1998) reviewed such provocative ideas of evolutionary biologists as Dawkins' "Selfish Gene" and Eldredge and Gould's "Punctuated Equilibria" (Eldredge and Gould 1972) and also relativized the meaning of adaptationism (p 95: "…organisms may not be as exquisitely fine-tuned to their environments…")

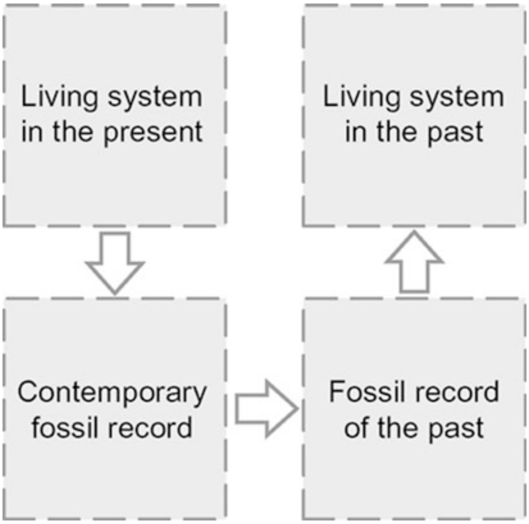


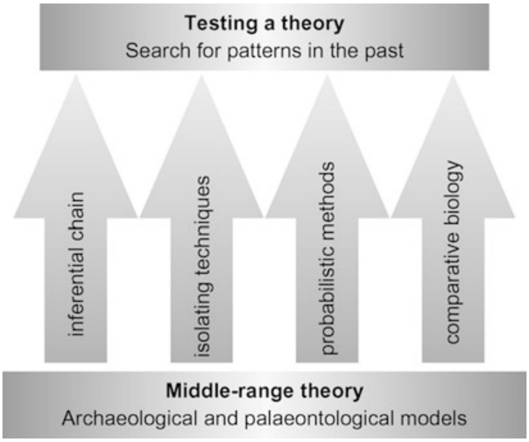
Fig. 1 Linking the past and the present. Interpreting the fossil record and reconstructing life in the past depend on the understanding of the process of transformation during fossilization. This is inferred by observations of contemporary fossil information or the way in which observable behavior in the present would be visible in the fossil record (After Foley 1987)

in our evolutionary thinking. Therefore, no one should forget that there exists a possibility of overstraining positivism, thus using only verified results as a basis for the interpretation of our findings. *Actio-reactio* thinking is of course essential and the *only* way of doing science in general, but the danger of storytelling in paleoecology is acute (Henke 2010). Scientists are at risk of delivering explanations for adaptations which could be true, but actually might not be (see later). It is questionable whether the equation *Bauplan : environment* = 1:1 is satisfied.

Foley (1978) linked the past and the present by invoking Binford's (1977, 1981) *middle-range theory*. This is actually an assemblage of theories that link observable aspects of the past to processes operating today and permit inferences about the conditions of geological and biological systems in the past. Such observations must be linked to observable past phenomena (i.e., an anatomical element) (Fig. 1). The connecting piece between a theory (deductions and predictions from a basis of axioms) and the data is the *model* (which describes and predicts the variation and structure of phenomena derived from theoretical principles).

Foley (1987) also points out that there are different levels of model building, depending on behavioral (predepositional) and geological (postdepositional) factors. Furthermore, identical records might be produced by different behaviors (Hill 1984; Foley 1987), so the *overlap* of different models has to be taken into consideration. Four pathways are very useful for testing a theory in order to reduce the pure reflection of contemporary ideas: (1) a careful analysis of each link in an inferential chain; (2) like Binford (1981) not following the broad trend, but rather looking for small details that might appear comparatively insignificant; (3) the isolation of processes that may result in similar results and assigning (theoretically/experimentally) the probabilities of various outcomes; and finally, (4) the comparative biological approach, which investigates patterns of interspecific and intraspecific variations that can be used to correlate biological variables (Fig. 2).

Fig. 2 Implications of the middle-range theory: a summary of pathways to the past (Modified from Foley 1987)



Ecology and Cladistics

The a priori assumption that a particular character (or character state) is the result of a particular evolutionary process may lead to far greater problems of circularity than does the incorporation of these characters into a global estimate of evolutionary history (Luckow and Bruneau 1997, p. 150). These authors infer that the exclusion of ecological information from a phylogenetic analysis when testing ecological hypotheses is not only unnecessary but also "undesirable." Luckow and Bruneau (1997) justified their arguments by concluding that character exclusion would partition the data in an arbitrary way and that discrete homology statements would get lost.

Abiotic Factors

Throughout natural history, the physical conditions of the Earth have had a strong influence on evolution, adaptive or otherwise, and consequently on human evolution (Dearing et al. 2006). Environmental changes shape the habitats and the evolutionary "fates" of living systems (see also Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). One fundamental aim of evolutionary biology is to understand and reconstruct the interaction of physical environmental stimuli and the survival of organisms – even in human evolution (Potts 2012; Bailey et al. 2011). Wegener (2005, p. 222) wrote: "Only by summing up all fields of the geosciences may we hope to find out the "truth," this means determining a picture that integrates all known facts in the best order and which seems to represent the utmost probability; even then we have to be aware that each discovery, regardless of which scientific field it emanates from, may modify the result" (translated by the authors). Earlier acceptance of this neglected genius' appeal for an adequate scientific network might have accelerated the unraveling of the Earth's physical secrets.

Geological Influences

Volcanism

In the truest sense of the word, volcanoes put pressure on their environments. Usually eruptions have a localized but strong influence. However, tephra (ejecta, e.g., ash or pumice) and lava do have the potential to modify water and soil chemistries, thereby eliminating or modifying habitats over wide areas. Occasionally they also support the conservation of important fossil footprints.

Including sea floor and continents, about 80 % of the Earth's surface has been produced by ascending melted rock, primarily at plate boundaries. Volcanic material creates a useful (though blurred) perspective on the Earth's interior. The Earth's lithosphere also delivers nutrients, chemical resources, and minerals (Press and Siever 1995).

Feibel (1999) investigated eruptive activity in the Turkana area of northern Kenya and concluded that the higher assumed rate (38 events per 240,000 years) indicates one significant eruption per 6,300 years. Massive eruptions can also cause global impacts since they glut the atmosphere with climate affecting aerosols. Rampino and Shelf (1992) discussed the controversial idea of the Mount Toba explosion 74,000 years ago, which might have produced a sharp cooling and consequently a temporary shift to glacial conditions. Even today volcanoes are able to paralyze parts of *Homo sapiens*' "modern life" if you imagine the eruption of Iceland's Eyjafjallajökull and ash-cloud-induced air-traffic breakdown in Northern and Middle Europe in 2010.

Tectonic Aspects

Faulting within local sedimentary basins, continental plate movement, and highland formation through uplift may greatly affect terrestrial habitats (Chernet et al. 1996; Trauth et al. 2007; King and Bailey 2006). Between 16 and 12 Ma, the Eurasian and the Afro-Arabian continental plates moved and allowed an exchange of the flora and fauna, e.g., an exodus of early African apes (Potts 2003). Between 7.0 and 5.0 Ma, the Atlantic Ocean and the western end of the Mediterranean were temporarily separated as Africa drifted northward. Here, a periodic drying and flooding of the Mediterranean basin occurred and huge salinity deposits were built up. Western Eurasia dried out due to an evaporation and salinization phenomenon. Between 4.5 and 3.0 Ma, the Isthmus of Panama was formed by the contact of continental plates and the following uplift (Stanley 1995). One result was the strengthening of the conveyor belt of Atlantic Ocean currents: the North Atlantic was "watered" by the warm Gulf Stream. The initiation of ice ages in the Northern Hemisphere during the Late Pliocene can be explained by the development, over 36 Ma, of isolation of the Arctic Ocean caused by a high-salinity, warm, sinking, and returning current (Stanley 1994).

Rift Valley formation in eastern Africa and the uplift of western North America and the Tibetan Plateau are examples of drying and cooling effects. Models of general circulation show that when major air currents are divided by elevated plateaus, the air is altered due to winter cooling and summer heating, causing high- and low-pressure areas to form over landmasses far from the plateaus (Ruddiman and Kutzbach 1989). One consequence is a greater seasonal variation and also the creation of seasonal monsoons. The overall effect is a cooler and drier global climate (Ruddiman et al. 1989). Even geochemical weathering on rocks can be traced back to uplifts: enhanced monsoons, steepening river gradients, and faster erosional rates increase weathering. Raymo and Ruddiman (1992) suggested that global cooling might result from the deposition of carbon from the highlands into the ocean as well as from weathering responses. A consequence would be a reduction in carbon dioxide and its removal from the atmosphere. The heat-retaining function of carbon dioxide as a major greenhouse gas would disappear as a result. Another effect occurs on the leeward sides of uplifted regions: upland depletion of air moisture and precipitation cause rain-shadow drying, a phenomenon partly responsible for the aridification of the area to the east of the African Rift Valley compared with its western counterpart.

Another possibility is that the shapes of sedimentary basins are modified by the local impact of earthquakes. Availability of water to the local biota is obviously a very important factor, so the changes of fluvial systems by intrabasin faulting mechanisms are also a matter of paleoecological discussion.

Eastern Africa is a superb example to illustrate intracontinental rifting phenomena. During the Cenozoic, a system of continental rifts developed from the Red Sea and the Gulf of Aden in a southward direction from the Afar region of Ethiopia, which is a triple junction where three developing tectonic plates come together (Figs. 3 and 4; Table 3). Such phenomena are widespread. A former triple junction existed where Africa and northern and southern America came together. The Amazon, the Mississippi, and the Niger all represent rivers that run through "failed rifts." Afar is characterized by three spreading zones and represents a small portion of oceanic crust that has been uplifted and is now part of the continent (Stanley 1994).

Climatic Influence

Cycling Planet Earth

The Milankovitch cycles (Rowan and Reed, chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1) are a consequence of the changing gravitational pull of other planets. Variation in solar heating, which is related to astronomical cycles that alter the orientation and shape of the Earth's orbit around the Sun, is attributed to these periodic oscillations. The distribution and strength of solar radiation change over the globe in periods of 19, 23, 41, and 100 thousand years (Hewitt 2003). How can these periods be detected? Oxygen isotopes are documented in the deep-sea record and represent measurements of the global ice volume, ocean temperature, and evaporation. Around 3.0–2.5 Ma, the amplitude and frequency of δ^{18} O oscillation changed significantly. Northern Hemisphere glaciations and greater aridity in the tropics both correspond to this pattern. Between 900 and 600 ka, the effects of 100,000-year-long cycles of glacial forming and interglacial warming came into play (Hewitt 2003).

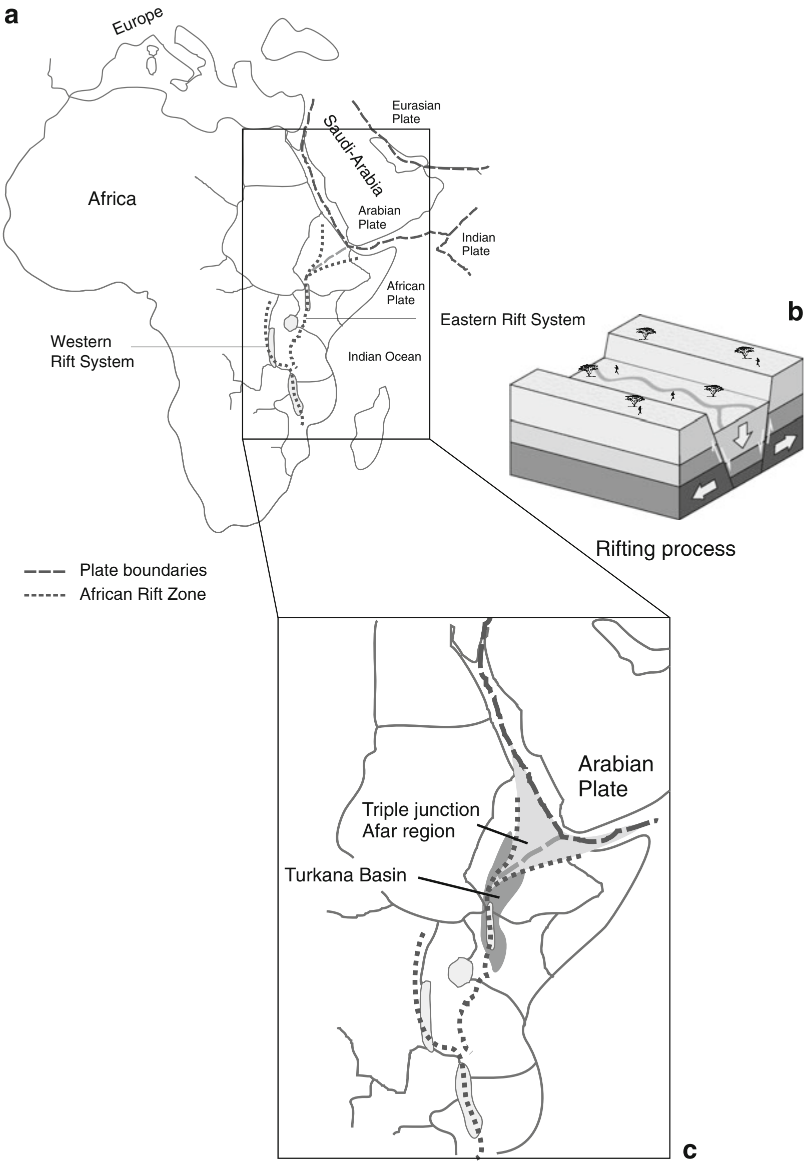


Fig. 3 African Great Rift Valley system (**a**) and rifting process (**b**) with accentuation of the Afar triangle and the Turkana basin (**c**)

The 23,000-year cycle of the Earth's rotational axis intensifies African monsoons, and the millennial-scale instability causes North Atlantic iceberg discharge. This involved huge masses of ice rafting and melting and a decrease of ocean salinity. Taylor et al. (1993) and Bond et al. (1997) traced this phenomenon back to

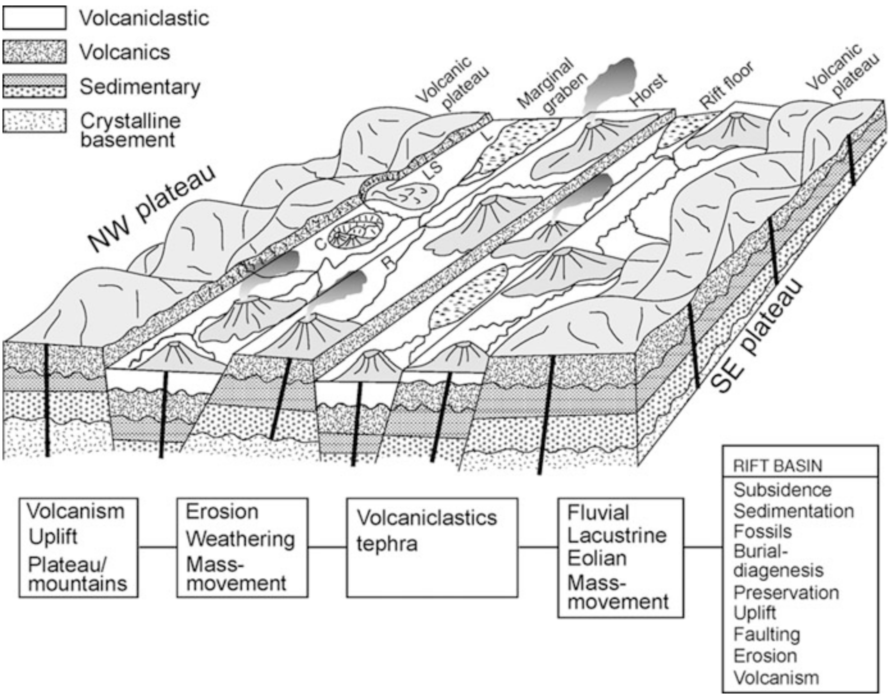


Fig. 4 Schematic representation of tectonism, volcanism, and sedimentation processes within the Ethiopian Rift System (WoldeGabriel et al. 2000)

decade- to century-scale fluctuations between near-glacial conditions and interglacial warmth. Raymo et al. (1998) and McManus et al. (1999) linked these conditions to the Late Pleistocene and Early Holocene.

Well-defined cycles are not necessarily well separated in terms of amplifying and buffer mechanisms. Their interactions show complex patterns, as Clemens et al. (1996) and Paytan et al. (1996) have demonstrated. Furthermore, Potts (2003, p. 365) stresses that "major environmental shifts occurred episodically throughout the Quaternary and did not necessarily coincide exactly with maximum changes in temperature, moisture, or any other single factor." Lister and Rawson (2003) called attention to the rise and fall of sea level, one major effect of the climatic ups and downs: over the past 600,000 years, fluctuations of up to 120 m are documented. Inundations as well as the exposure of continental shelves created new barriers or pathways. Like others Maslin and Christensen (2007) assume coherence between, on the one hand, extreme climatic variability caused by tectonic changes and orbital forcing and, on the other hand, speciation and dispersal events in human evolution. Ann Gibbons brought together several researcher's suggestions linking climatic variability to major events in human evolution like speciation or the development of modern stone tool technologies like the Acheulean (Gibbons 2013) under the title of "How a fickle climate made us human."

Table 3 The Ethiopian Rift System and some important paleoanthropological sites

Areas with paleoanthropological sites	Location within the rift	Sedimentary environments	Age of tuffs	Number of tuff beds/Ma (preserved)	Tuffs; percentage of stratigraphic section	Percentage of tuffaceous sediments in stratigraphic column	Hominid species
Shungura Usno Fejej	Omo rift	Lacustrine, fluvial, overbank	4.1–1.39 Ma	13	9	Estimated at 70	*A. afarensis*, *A. aethiopicus*, *A. boisei*, *H. habilis*, *H. erectus*
Konso-Gardula	Southern MER (Main Ethiopian Rift)	Fluvial	2.0–1.35 Ma	~4	5	95	*H. erectus*
Gademota (Middle MSA)	Central MER	Colluvium, paleosol	35–1.81 ka	3	n.d.	n.d.	*H. sapiens*
Gadeb	Eastern rift shoulder, Central MER	Lacustrine, fluvial	2.51-ca. 0.7 Ma	>2	~12	Estimated at 50	*H. erectus*

Melka Kunturè	Central MER	Fluvial	< or = 1.5 Ma	5	n.d.	n.d.	*H. erectus*
Kesem-Kebena (K-K6)	Northern MER	Lacustrine, fluvial, lacustrine	1.04–1.0 Ma	3	38	62	*H. erectus*
Middle Awash	Southern Afar	Fluvial, overbank, lacustrine	4.38–4.29 Ma	>20	5	40	*A. ramidus*, *H. erectus*, *A. garhi*
Hadar	West-central Afar	Fluvial, overbank, lacustrine	3.4–3.18 Ma	5	<5	Estimated at 40	*A. afarensis*, *H. erectus*
Gona	West-central Afar	Lacustrine, deltaic, fluvial	2.94–<2.52 Ma	>4	<5	Estimated at 40	None

Modified from WoldeGabriel et al. (2000)

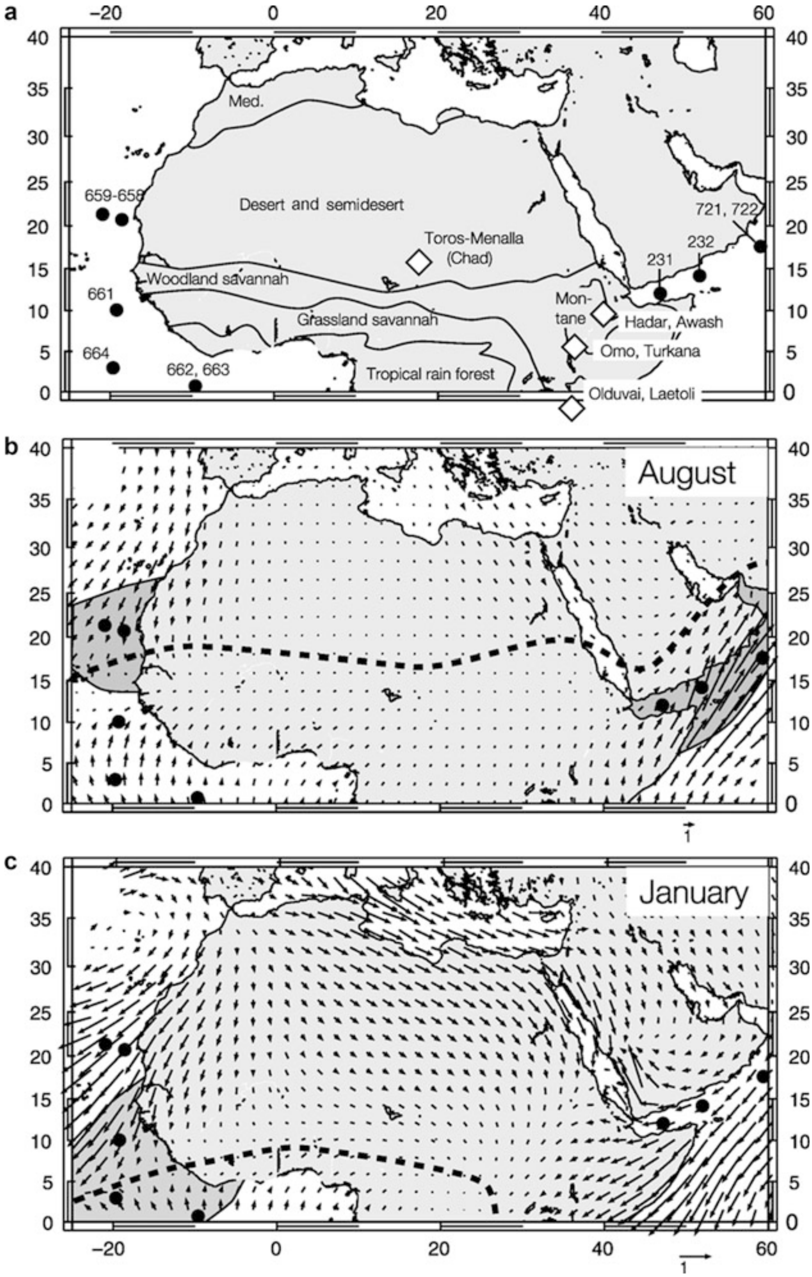


Fig. 5 (continued)

Our Planet's Oceans

The Earth's climates were much wetter and warmer before Middle Eocene times, and deciduous and evergreen forests dominated the natural scenery. Antarctica was full of temperate rain forests, and Arctic landmasses were covered with trees (Askin 1992; Denton 1999). A strong seasonality and a general lack of aridity reduced the occurrence of grasslands and deserts. Sea ice and glaciers were limited in their volume expansion (Ruddiman and Kutzbach 1991). The world's oceans were about 10 °C warmer at depth than today. Furthermore, the atmospheric temperature gradient – from the equator to the pole – was much smaller than today (Savin et al. 1975; Shackleton and Boersma 1981).

This changes when throwing a glance at the recent situation. Since the Middle Eocene, global climate has cooled down. Shackleton (1995) discussed the essential global paleoclimatic change at 2.95–2.52 Myr and the beginning of the oscillating ice ages. Over the past 0.95 Myr, each glacial maximum was on average 5 °C cooler than today and the planet was drier, e.g., much of Northern Europe was covered by tundra and Africa was drier (Denton and Hughes 1981; Denton 1999).

Another Unique Continent: Africa

deMenocal (2004) gave us a very useful overview of the African climate: as Fig. 5 demonstrates, the combination of the seasonal migration of the intertropical convergence zone and the African monsoon causes a highly seasonal range of North African rainfall. In the boreal summer, heat over the North African land surface, centered near 20° N, draws moist maritime air from the equatorial Atlantic into western and central subtropical Africa. Accordingly, woodland and grassland savannas flourish (Hastenrath 1985; Harris 1980).

Based partly on topographic rain-shadow effects, summer rainfall in East Africa is very variable. It is also related to the westerly airstream of the African monsoon (Nicholson 1993). East Africa's subtropical rivers, such as the Omo and the Nile, are drained by the summer monsoonal runoff via the capture of moisture by Ethiopian and Kenyan Highlands. On the other hand, relative to adjacent oceans, Asian and African landmasses become cooler, and a reversion of the atmospheric circulation comes about (deMenocal 2004).

Prospero and Nees (1986) showed that the changes of subtropical African summer rainfall are closely tied to West African dust export to the Atlantic. Additionally, these modifications have been linked by Giannini et al. (2003) to anomalies of the sea-surface temperature. Fig. 5b demonstrates that Indian

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Fig. 5 (**a**) Regional map of North Africa vegetation zones, locations of DSDP and ODP drill sites (*filled circles*), and locations of selected African mammal fossil localities (*open diamonds*). (**b**) Boreal summer (August) surface wind stress (unit vector = 1 dyn/cm^2), intertropical convergence zone (ITCZ, *heavy dashed line*) location, and boundaries of seasonal tropospheric dust plumes off NW Africa and NE Africa/Arabia. Dust plume contours were derived from haze frequency data. (**c**) Boreal winter (January) surface wind stress (unit vector = 1 dyn/cm^2), ITCZ location, and boundary of the seasonal tropospheric dust plume off NW Africa (Reprinted from deMenocal (2004), with permission from Elsevier.)

monsoon surface winds are interconnected with summer dust plumes of Arabia and Northeast Africa (Nair et al. 1989). These winds carry mineral dust to the Arabian Sea and the Gulf of Aden. The study of mineralogical and sedimentological data reveals that wind-borne detritus "from these sources comprises the dominant source of terrigenous sediment to the eastern equatorial Atlantic and the Arabian Sea" (deMenocal 2004, p. 7).

Marine Paleoclimatic Records

The last (ca.) 5 Myr, during the Late Neogene, showed progressive steplike increases in African aridity and periodical arid-humid climate cycles. This conclusion can be drawn from marine sediments accumulating off the western and eastern margins of the subtropical North African region. The isolation of the Atlantic basin via the Isthmus of Panama and the following gradual onset of high-latitude glacial cycles at 3.2–2.6 Ma seem to have influenced African climate variation patterns (Haug et al. 2001). The onset of glacial ice rafting and modest 41-kyr glacial cycles after 2.8 Myr caused Plio-Pleistocene cooling at high latitudes. Another step was a shift toward cooler conditions and, after ca. 1.6 Myr, higher-amplitude 41-kyr cycles after 1.2–0.8 Myr (Shackleton et al. 1984).

Variability of subtropical African paleoclimate: deMenocal (2004) summarized the patterns of marine sediment records of Plio-Pleistocene eolian export from West and East Africa:

- The variability of orbital-scale African climate variability persisted throughout the entire interval (and in some cases extending into the Miocene and Oligocene).
- The onset and amplification of high-latitude glacial cycles was closely linked to the onset of large-amplitude African aridity cycles.
- A gradually increasing increasing of eolian concentration and supply (flux) after 2.8 Myr.
- At 2.8 (±0.2), 1.7 (±0.1), and 1.0 (±0.2) Myr, there were steplike shifts in the amplitude and period of eolian variability.
- There is evidence for 10^4- to 10^5-year "packets" of high- and low-amplitude paleoclimatic variability which were paced by orbital eccentricity.

deMenocal (2004, p. 8) described the marine record as "a succession of wet-dry cycles with a long-term shift toward drier conditions, punctuated by step-like shifts in characteristic periodicity and amplitude." de Menocal (1995) interpreted subtropical African climate prior to 2.8 Myr as varying at the 23- to 19-kyr period, mainly as a result of Asian monsoonal variability. At 2.8 (±0.2) Ma, there was a shift toward climate variation periods longer than 41 kyr, and after 1.7 (±0.1) Myr, the cycles lengthened again, and an eolian variability shift toward longer- and larger-amplitude 100-kyr cycles after 1.0 (±0.2) Myr occurred. The onset and growth of high-latitude ice sheets and cooling of the subpolar oceans were synchronous with these shifts in the African eolian variability (Shackleton et al. 1990), and there was a coupling between high- and low-latitude climates after the glaciation onset near 2.8 Ma (deMenocal 1995).

Dupont and Leroy (1995) showed that a pollen record from site 658 documents the phenomenon of greater variability and progressively xeric vegetation after ca. 3.0 Myr and concluded that a shift toward a drier and cooler African climate occurred during glacial maxima. The pollen record correlates with oxygen isotopes, indicating that large global ice volume and deep-sea temperatures correspond to aridity. These authors conclude that a comparison of short-term fluctuations of periods before and after 2.5 Myr demonstrates "that obliquity forcing of northwestern African climate started with the first large glaciations in the Northern Hemisphere" (p. 297).

Which phenomenon is the fundamental impulse generator for African climate variability? The Plio-Pleistocene succession of sapropel layers in the Mediterranean Sea could be interpreted as a consequence of orbital precession (Hilgen 1991). Enhanced monsoonal and Nile river runoff led to increased Mediterranean stratification and reduced ventilation of the deep eastern basins (Rossignol-Strick 1985). During these humid periods, organic-rich layers were deposited. However, another stimulating factor could be a covariation of African climate with the high-latitude climate cycles at the 41- and 100-kyr periodicities, which is what marine sediments actually suggest.

deMenocal (1995, 2004, p. 10) tried to reconcile the two different points of view "by acknowledging that precession was the fundamental driver of African monsoonal climate throughout the late Neogene, but that high-latitude glacial cooling and drying effects were superimposed on this signal only after 2.8 million years."

Physical (Paleo)geography or the Beauty of Mosaics

The African continent extends virtually equidistant into both the Southern and the Northern Hemispheres. It includes about 20 % of the world's land surface and stretches 8,000 km from north to south. The configuration of the bordering oceans and landmasses has remained almost the same from the Early Pliocene up until today (O'Brien and Peters 1999).

Based on the pioneering work of Lobeck (1946); O'Brien and Peters (1999) subdivided Africa into different physiographic regions (Fig. 6). In Low Africa, during most of the Pliocene, all of the interior basins may still have lacked outlets to the sea, a condition not existing today. Prerift Africa's (Miocene-Pliocene) interior basins and associated drainage systems are nowadays etched by old deltas, strandlines, old terraces, and alluvial deposits. This might indicate (at least) seasonally expansive internal lakes, e.g., the Paleolake Congo. This was probably a perennial water body up to at least the Late Pliocene, and its eastern catchment extended to the High Interior Plateau and the volcanic highlands of the Eastern Rift Belt (O'Brien and Peters 1999).

In the Oligocene, High Africa was tectonically driven by the African swell, which was active again in the Late Pliocene and Pleistocene. Different effects have

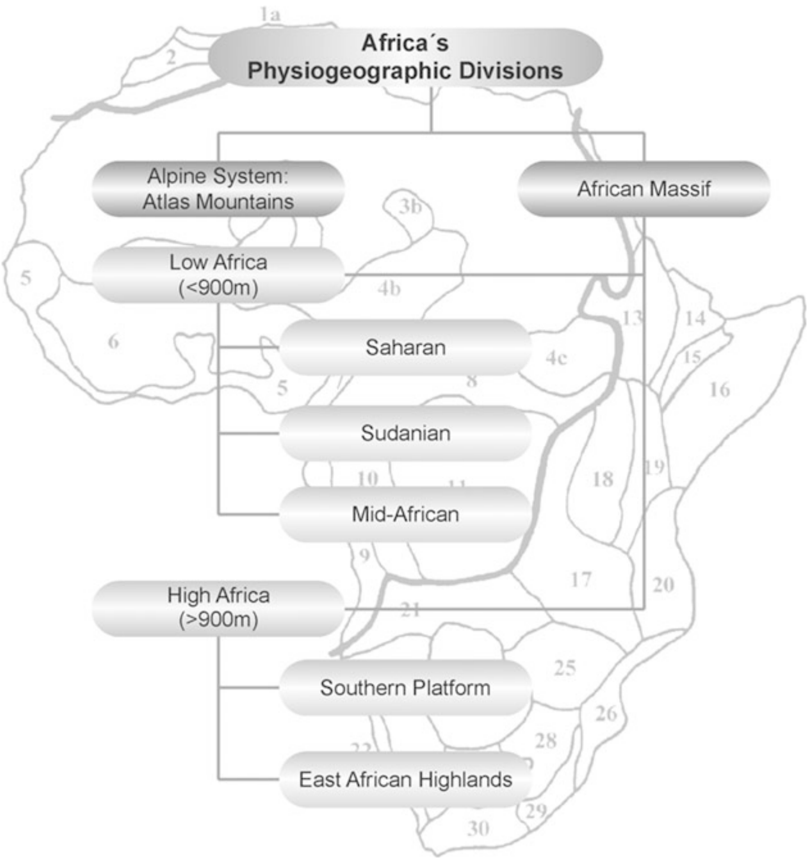


Fig. 6 Physiogeographical divisions of Africa (After O'Brien and Peters 1999)

influenced southern and eastern Africa: during the Late Pliocene, local environmental and increasing subregional fragmentation took place. During the Early as opposed to the Late Pliocene – up to 3.0 Myr – the rift grabens associated with doming were shallow and also at higher elevations than now (Brown 1995). The Ethiopian Massif was probably lower than now, while the High Eastern Interior Plateau may have been higher (Feibel 1999). Between 3.0 and 2.0 Ma, an uplift of rift shoulders by 1,000–1,500 m and a concomitant major subsidence of rift grabens occurred: (1) first in the Eastern Rift Belt areas and in the Afar region and later (2) in the Western Rift Belt, where some of the uplifted flanks rose to 4,000 and more meters above sea level (Partridge et al. 1995a, b). The eastern drainage perimeter for the Congo Basin was established by the escarpment mountains of the Western Rift Belt, which also caused a diversion of the westward drainage from the Eastern Rift Belt and the Interior Plateau, into the Sudd. The Rift Valley domain of the East African Highlands was particularly perforated by active volcanoes (O'Brien and Peters 1999).

Africa's Southern Platform was formed by subsidence events resulting in local fragmentation of the environment (exceptions: areas immediately adjacent to subsided or uplifted margins) and by broad-scale regional uplift. The Southern Platform was apparently lower in elevation than nowadays by some 200 m in the southern escarpment mountains and by as much as 1,000 m in the extreme southeast. The Transvaal, however, was somewhat higher than today (maybe by about 400 m). Furthermore, the paleolakes of the Southern Platform are of special interest for hominid ecogeography (e.g., Makarikari). The grabens of the Western and Eastern Rift belts in the East African Highlands contained intermittent rivers and lakes. Lake Malawi, however, obtained its present shape only at the end of the Pliocene (Partridge et al. 1995b; O'Brien and Peters 1999).

Biotic Factors

Together, abiotic factors build a framework for living spaces that frequently harbor more than one population (Ziegler 1992). These spaces are called *biotopes*, with their enclosed organismic communities characterized as *biocenosis*. These often include highly adapted and specialized species in numerous ecological niches; together they build the so-called ecosystems or *biomes*. The goal of paleoecologists is to reconstruct these systems or paleoenvironments based on organic and inorganic remains.

In the following section, we concentrate mainly on fossils and their interpretation and on the factors that influence them and thus have to be analyzed when reconstructing paleoenvironments. We touch on questions of *postmortem* processes, stratigraphic research, and coevolution. Due to the fact that we spotlight hominid and accordingly terrestrial evolution, we omit an extensive debate on plant fossilization and exclude aquatic ecosystems.

Fossils

A fossil is any remain or trace of any organism from all past periods. They are the key elements of paleontology and consequently of paleoanthropology and paleoecology and act as *containers* or *archives* that preserve information over a long period. Scientists who deal with fossils have to find the right *tools* to open and unravel the secrets lying within. The following paragraphs illustrate some of these "tools" and enlighten several approaches of paleoecological research.

What Happened *Antemortem* and What *Postmortem*?

It is unlikely that an organism will be preserved through time after death. Less than 1 % of all species of organisms are handed down to us (Ziegler 1992; deMenocal 2004), especially in terrestrial and tropical conditions, also in the case of hominoids (Carroll 1988; Martin 1990; Stanley 1994; Andrews 1990). Due to this, the density of relevant paleoanthropological fossils is very low – approximately one fossil per one

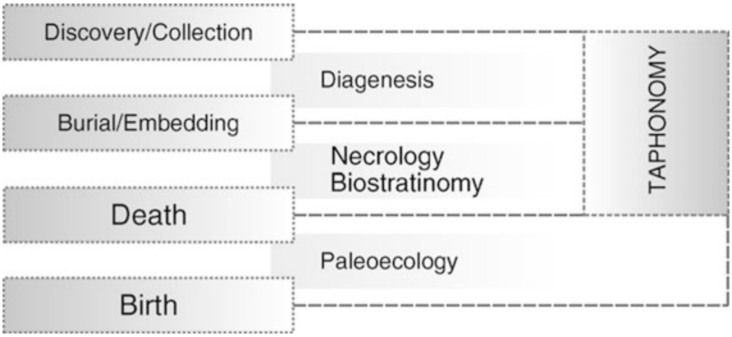


Fig. 7 Four key events in the history of a fossil and the related paleontological disciplines (After Lawrence 1968)

hundred generations – and there are a lot of gaps that affect the phylogenetic and ecological reconstructions scientists strive for (see later). Besides this, most fossils are fragmentary or incomplete and require reconstruction by means of all available methods, now including 3D reconstruction using CT, MRT, or surface scanning (Weber, chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1). Additionally, researchers have to consider the limited erosion of noteworthy ancient fossil sites on the African continent, since most areas are covered with tropical forest, as well as the political and financial circumstances that impede excavations on the other hand.

Every fossil contains a great deal of information on the evolutionary history (phylogeny), physical organization (morphology), and lifestyle (ecology) of the populations the organism once belonged to. Under ideal circumstances, it is possible to extract most of this information by careful analyses of the taphonomic and diagenetic processes involved. *Taphonomy*, as a special field of paleontology, represents the description and causal analysis of all factors that influence an organism after death (necrology and biostratinomy) (Fig. 7) and subsequently all processes of embedding and fossilization (Efremov 1940; Lyman 1996; Grupe and Harbeck, chapter "▶ Taphonomic and Diagenetic Processes," Vol. 1). In contrast, *diagenesis* characterizes only the biological, physical, and chemical alteration of the mineralogical elements affecting fossil-bearing sediments and is part of taphonomy and the lowest grade of rock metamorphism (Stanley 1994; Lyman 1996; Conroy 1997).

The possibility that an organism will be fossilized after death – its transition from the bio- to the lithosphere – depends on many environmental factors (Foley 1978; Henke and Rothe 1999). With few exceptions, the soft tissue – if not eaten by predators or scavengers – undergoes the physiological processes of decomposition and decay in the first phase after death (necrology), and normally only hard materials like the teeth, bones, shells, and rarely scales and horn are suitable for being mineralized and thus fossilized. The most important participants in this process are calcium in the form of calcite and aragonite ($CaCO_3$), bone apatite ($Ca_5(OH)(PO_3)$), silicic acid-skeletal opal (SiO_2), chitin, cellulose, and scaffold proteins (spongine, creatine).

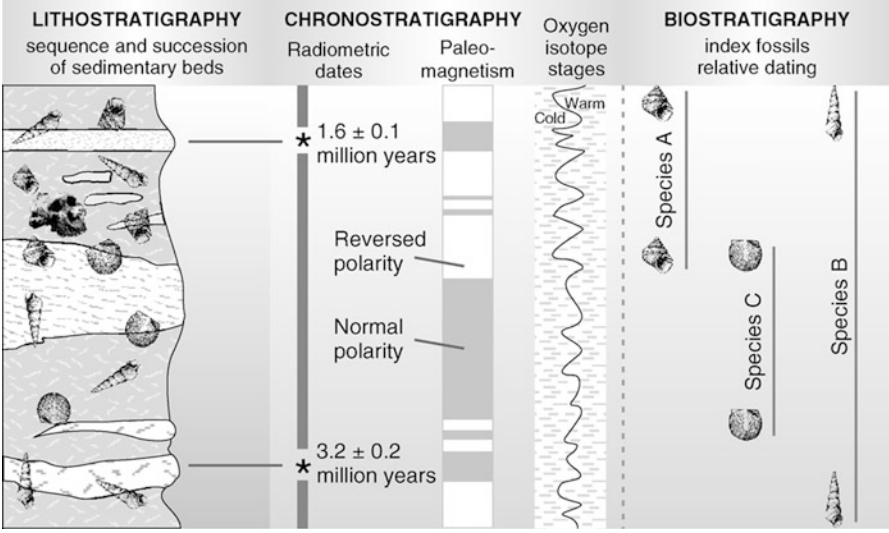


Fig. 8 Three essential components of the study of fossils in context (Adapted from Behrensmeyer 1992)

Who Are You? Where Do You Come From? What Brought You There?

The only way to reconstruct ancient ecosystems is to examine the fossil record and elucidate the internal and external influences that led to the life-forms. Following Etter (1994), there are three crucial requirements that have to be fulfilled when analyzing fossils:

1. Accurate determination and systematic classification of the collected specimen
2. Putting all investigated profiles in a temporal and stratigraphic order as precisely as possible
3. Understanding the ecological context and the specific adaptations of the organisms that enable it to live in particular environments

In brief, paleontologists and paleoanthropologists, respectively, have to study fossils in context to understand the processes occurring in interrelated evolving systems (Fig. 8).

Who?

Taxonomic classification is not only essential but also complicated and depends on whatever evolutionary theory, species concept, and taxonomic approach the researcher prefers (Delson 1990; Foley 1978; Tattersall 1992, 1996; Wood 1992, 1996; Wood and Collard 1999; Wolpoff 1999; Wheeler and Meier 2000; Sarmiento et al. 2002). All these questions go beyond the scope of this chapter and are discussed elsewhere in these volumes (Ohl, chapter "▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms," Vol. 1). Academics need to overcome the subject-object problem (Stadler et al. 1977; Vogel 2000) when analyzing how we "became human" or even when assembling or disassembling new genera or species – not to mention new hypotheses or theories – as soon as possible after finding new hominid remains. In the words of Eric Delson: "The paleoanthropology community must look quite Pavlovian to outsiders – we all drool predictably every time a new fossil is discovered" (Delson 1997, p. 445). Obviously, new fossil findings complicate the puzzle of primate and hominid evolution (Foley 1991; Tattersall 1992, Marks, chapter "▶ Genetics and Paleoanthropology," Vol. 1).

Since Darwin's ideas about natural selection and his groundbreaking theory of evolution via selective forces were published in 1859, much has been learned about the processes that generate species and the debate is still in progress. Using the individual specimens that constitute the fossil record, we can indirectly scrutinize ancient organic systems at definite points in time ("semaphoronts" sensu Hennig 1982). One affiliated evolutionary theory, "punctuationism" (antonym: gradualism) postulates rapid evolutionary development at the nodes of the "Tree of Life" and long periods (branches) with slow rates of evolutionary change. Associated with the latter is a crucial problem of fossil research, for the chance of finding and moreover identifying "node fossils" (once called "missing links") is significantly lower than of finding "branch fossils." Another accompanied question arises: Are "node fossils" detectable at all or are we entangled in fossils that show mosaic-like plesio- and apomorphic character stages making it nearly impossible to fix a borderline between species – even genera? However, human evolution is strongly embedded within the framework of evolutionary biology and has to be seen as a chain of adaptive radiations (Foley 2002) and extinction events.

Where and When?

One of the most important factors when reconstructing ancient ecosystems is the time dimension and thus the absolute and relative determination of age (dating). Stratigraphers subdivide sediment layers chronostratigraphically and put them in a hierarchic system (Table 4; Fig. 9). Each unit within a stratigraphic system has been defined by means of a basal Global Standard Section and Point (GSSP) by the International Commission on Stratigraphy. Absolute dating, or chronometrics, is done by direct chemical (e.g., amino acid racemization) or physical (e.g., radiometric, thermoluminescence, magnetism) analyses of the bone tissue, rocks, or fossil material in the facies (as the sum of all primary rock characteristics that incorporate inorganic (lithofacies) and organic (biofacies) elements) of interest, and different techniques attain different time depths (Conroy 1997; Wagner and Richter, chapter "▶ Chronometric Methods in Paleoanthropology," Vol. 1). Relative dating methods are tightly related to the theory of, or directly on, *stratigraphy* and the idea of marker fossils, primarily developed by Nicholas Steno, a Danish anatomist, and upgraded by William Smith (alias "strata Smith"), an eighteenth-century English engineer (Ziegler 1992; Stanley 1994; Rothe 2000). Their perceptions led to three principles of sedimentation: (1) younger deposits overlie the older ones from the bottom up; (2) in the initial state, all layers are approximately horizontal; and (3) sediments extend laterally and can be parallelized over large areas (Rothe 2000). A further important law was

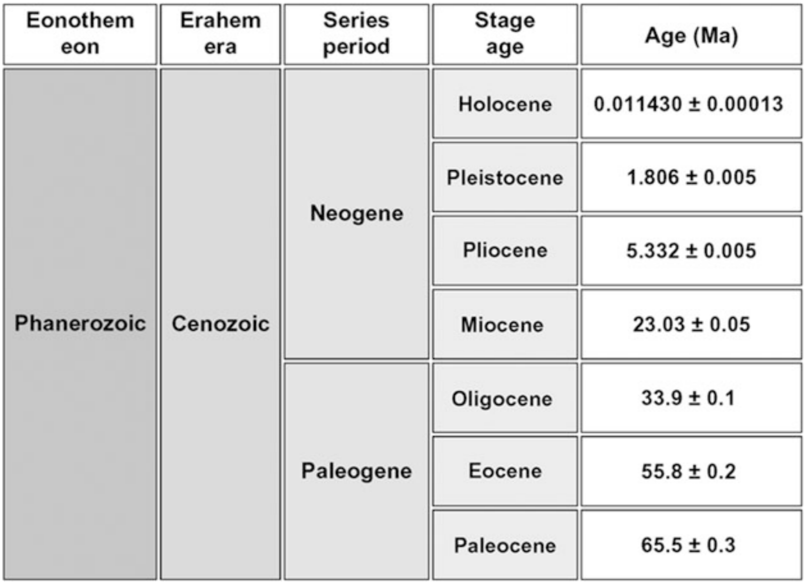
Table 4 Summary of the categories and unit terms in stratigraphic classification

Stratigraphic categories	Principal stratigraphic unit terms	Equivalent geochronological units
Lithostratigraphic	Group	*Note*: if additional ranks are needed, prefixes "sub" and "super" may be used with unit terms when appropriate, although restraint is recommended to avoid complicating the nomenclature unnecessarily
	Formation	
	Member	
	Bed(s), flow(s)	
Unconformity bounded	Synthem	
Biostratigraphic	Biozones	
	Range zones	
	Interval zones	
	Lineage zones	
	Assemblage zones	
	Abundance zones	
	Other kinds of biozones	
Magnetostratigraphic polarity	Polarity zone	
Chronostratigraphic	Eonothem	Eon
	Erathem	Era
	System	Period
	Series	Epoch
	Stage	Age
	Substage	Subage (or age)
	(Chronozones)	(Chron)
Other (informal) stratigraphic categories (mineralogical, stable isotope, environmental seismic, etc.)	-Zone (with approximate prefix)	

Murphy and Salvador (1999)

established by Johannes Walther, a German geologist and student of Ernst Haeckel, who based his inferences on the Swiss geologist Amanz Gressly's fundamental contributions on stratigraphy in the eighteenth century and stated that the vertical succession of facies reflects lateral changes in past environments (Cross and Homewood 1997). Stratigraphic research can be roughly divided in three parts that differ in materials and methods:

1. *Lithostratigraphy* deals with the sequence and succession of sedimentary beds to yield diachronic zones; only a few "key beds" are nearly isochronic (Behrensmeyer 1992; Stanley 1994).
2. *Biostratigraphy*, which is based on organismic evolution, shows overlapping zones by analyzing facies-specific marker or index fossils that can be deemed as



Eonothem eon	Erahem era	Series period	Stage age	Age (Ma)
Phanerozoic	Cenozoic	Neogene	Holocene	0.011430 ± 0.00013
			Pleistocene	1.806 ± 0.005
			Pliocene	5.332 ± 0.005
			Miocene	23.03 ± 0.05
		Paleogene	Oligocene	33.9 ± 0.1
			Eocene	55.8 ± 0.2
			Paleocene	65.5 ± 0.3

Fig. 9 Geological time scales (Dates refer to the International Commission on Stratigraphy 2004)

isochronic (Stanley 1994). Age estimations become more precise, the more closely index fossils are related (Behrensmeyer 1992). The life span of a fossil species, referred to as its “zone,” ranges from the first appearance of that species until a subsequently following species replaces it. Biostratigraphic time scales are often bound to a specific area. Both approaches offer the possibility of correlating sediments and time horizons continuously in regional areas (parastratigraphy) and worldwide (orthostratigraphy).

3. *Chronostratigraphy*, rock layers (strata) are sequenced and classified by absolute dating methods.

Christian Leopold von Buch, an eighteenth-century German geologist, popularized the term “index fossils” as a marker for the correlation of contemporary strata, based on considerations by Charles Darwin and Charles Lyell concerning the irreversibility of changing morphologies through evolutionary time. Index fossils have to meet a number of requirements: (1) worldwide distribution, (2) rapid development that means a visible short time span of one species and evident morphological differences in comparison to other species, (3) high number of individuals, and (4) high chance of being preserved (Carroll 1988; Ziegler 1992). Obviously, marine organisms (plankton and nekton) are ideally suitable as index fossils, and for that reason paleontologists often focus on aquatic micro- and nanofossils to date sediments (e.g., foraminifers, diatoms). But macrofossils are also appropriate for stratigraphic positioning; these include the teeth (Kullmer 1999) and the hard tissues of smaller multicellular species (e.g., ammonites, graptoliths, conodonta). In addition to index fossils, there are also so-called “facies fossils” that are important for the characterization of a certain milieu with particular ecological conditions; early hominids fit in here. Problems for the chronological determination of strata are produced by geomorphological events like earthquakes, volcanism, dislocations, and disconcordance on the one hand and organism-induced disturbances like bioturbation and digging on the other.

A special case in stratigraphy is sequence or cyclostratigraphy, which corresponds to the global correlation of tectonically independent eustatic sea-level fluctuations that happen synchronically in the form of transgressions (sea level raises over supratidal area) and regressions (sea level falls under the lowest tide gage) that are reflected in terms of changing communities (terrestrial/aquatic) and graphical curves. Further methods of dating involve measurements of cyclic events, e.g., seasonal temperature changes, among others: paleomagnetism, palynology (microflora and microfauna, e.g., spores, pollen, ostracods, radiolarians), dendrochronology (counting annual tree rings), dentin annulations (counting tooth dentin layers), diverse luminescence dating methods, stable isotope analysis in ice- or deep-sea cores, and microfossils (Lee-Thorp and Sponheimer, chapter “▶ Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction,” Vol. 1). Investigations of paleolimnological detritus layers are a method developed by the Swedish scientist Baron de Geer in 1878 and known as the exploration of “varves” (Swedish term that stands for “periodical recurrence”), annual laminated sediments in paleolakes. These methods all lack a link to “absolute” time, i.e., there is, with the exception of tree rings, no determination of a “null varve,” a starting point (Rothe 2000). An overview of relative and absolute dating methods is given in Table 5.

What Context?

Biotic information may be obtained from body fossils that deliver morphological insights (comparative morphology) and from trace fossils that contain ecological information in the form of organic tracks and inorganic marks (ichnology, e.g., footprints of Laetoli). In the case of body fossils, attention should be paid to the immense differences between life, death, and fossil assemblages (Fig. 10). A biocenosis simply represents all living species, i.e., the extant “community” in an ecosystem; in contrast, paleobiological remains are differentiated into autochthonous (thanatocoenosis = death or indigenous assemblages, in situ communities) and allochthonous (taphocoenosis = fossil assemblages) extinct communities. The latter may be affected by minor transport events (parautochthonous) or represent a mixture of local species and species that are brought in. Differences between life and fossil assemblages may result from “displacement” of various kinds (transport, accumulation, disarticulation, etc.), scavenging, destruction of hard materials (bio-erosion, abrasion), obliteration of specific elements (calcite vs. aragonite), etc., all of which may lead to misinterpretation in terms of taxonomy and ecological and chronological placement of fossils.

However, even in contemporary communities, it is complicated to sort out decisive external and internal factors and to show which weighting each has on specific developments in an ecological system.

Table 5 An overview of dating methods (relative and absolute, no claim for completeness)

Dating methods	Description in brief
Relative dating methods	
Cation ratio	Geographical-dependent age determination of a rock by surface analyses (positive-charged ions in the varnish that is formed on a rock), very inaccurate
Cultural affiliation	Determination of temporal levels of tool industries, ceramics, etc. made by the temporal community in a certain area
Fluorine dating	Fluorine accumulates in bone material (fluorapatite) that is deposited in groundwater-leading layers, thus providing information on the past time after burial
Obsidian hydration analysis (OHA)	Obsidian absorbs atmospheric humidity; old artifacts show a thicker "rind" of hydrate than younger ones (dependent on external factors like soil type, climate, erosion, burning, etc.)
Patination	This technique is used when multiple artifacts of the same type are found in the same area and under the same conditions; several kinds of patina are related to time
Pollen analysis	The study of chronological vegetational history by using microfossils in a target area
Rate of accumulation	Rock layers accumulate over time; thus, the deeper the layer, the older (applies also for artifacts associated with layers)
Seriation	Changes in ceramic forms over time to reconstruct consistent patterns of cultural trait change
Varve analysis	The thickness and shape of annually laminated sediments in a specific ecosystem (mostly paleolimnological) account for composition, displacement, and climate
Fossils	"Zones" of organismic remains (mostly species) are determined to classify certain strata
Absolute dating methods	
Archeomagnetism	Determination of variations (intensity, direction) in the Earth's magnetic field
Astronomical dating	Analysis of the Sun's declination at the solstices
Dendrochronology	Counting annual tree rings in order to determine the age of wood and reconstruct seasonal conditions
Electron spin resonance	Artifacts/fossils are exposed to radiation that predictably changes the magnetic field of the object (nondestructable)
Thermoluminescence dating (TL)	When reheating artifacts, the emitted light of specific crystals is proportional to the amount of radiation absorbed since the material was last heated, thus, provides a method to date pottery, hearths, fire-heated rocks, and burned minerals
Optically stimulated luminescence (OSL)	Similar to TL, it uses light to innervate vacated electrons in sediments; comparisons could be made through sediments with a known amount of added radiation
Fission track	Uranium (^{238}U and ^{235}U) radioactive elements create fission tracks by spontaneous splitting of uranium atoms and therefore exposing high amounts of energy that destroy the crystal lattice in a mineral

(*continued*)

Table 5 (continued)

Dating methods	Description in brief
Oxidizable carbon ratio (OCR)	Soil bodies are analyzed to determine the linear progression of slow humus and charcoal recycling through time with an increase in readily oxidizable carbon and a decrease in the total amount of organic carbon
Potassium-argon dating ($^{40}K/^{40}Ar$)	The measurement of the accumulation of argon in a mineral over time
Argon-argon dating ($^{39}Ar/^{40}Ar$)	Comparison of the amount of ^{40}Ar and ^{39}Ar; ^{40}Ar is a stable isotope, thus does not decrease in time, whereas ^{39}Ar is radioactive and consequently decreases over time
Radiocarbon dating (^{14}C)	Age estimation for organic materials by measuring the disintegration of radioactive ^{14}C since an organism died; data indication is given by years before present (BP), whereas "present" means exactly AD 1950
Uranium-thorium dating ($^{234}U/^{230}Th$)	Comparison which uses the properties of radioactive half-life ^{234}U and ^{230}Th and measures the equilibrium between these elements and not the accumulation of a decay product
Aluminum-beryllium dating ($^{26}Al/^{10}Be$)	The ratio between aluminum and beryllium isotopes in the mineral quartz changes under cosmogenic radiation. The specific conditions of radiation must be previously determined
Uranium-lead dating Thorium-lead dating	The ratio of radioactive uranium and thorium isotopes to lead as decay product, dating of rock material with a tremendous time depth of billions of years
Rubidium-strontium dating	Stable isotope ratio $^{87}Sr/^{86}Sr$ is measured in rock material
Racemization	Amino acids as subunits of proteins are widespread in organisms; living organisms contain only l-amino acids (turn polarized light to the left); in dead organisms l-amino acids degrade stepwise to d-amino acids (turn polarized light to the right) until the amounts are equal; thus, the ratio between both conformations provides information about the age of a sample (5,000–ca. 200,000 years depth)
^{2}H, ^{13}C, ^{15}N, ^{18}O, ^{34}S stable isotopes	These isotopes are found for several reasons in different amounts in sample materials of different kinds and could be useful for agricultural, archaeological, ecological, nutritional, geochemical, or medical research

Floras, Faunas, and a Word on Coevolution

There is – and always has been – a constrained relationship between flora and fauna. Since the first algae produced large amounts of oxygen, completely changing the atmosphere, animals and plants have had different interdependencies, though there is a comprehensive pattern of coevolution. To put it simply, coevolution or mutual selection is the process of reciprocal influence exerted by entities (mostly species) in an ecosystem (Begon et al. 1998), e.g., predator–prey or parasite–host relationships. The association of insects that need nectar and plants that require pollen transportation presents a common example. In the case of primate evolution, Sussman (1991) hypothesized that primates evolved in conjunction with the radiation of angiosperm

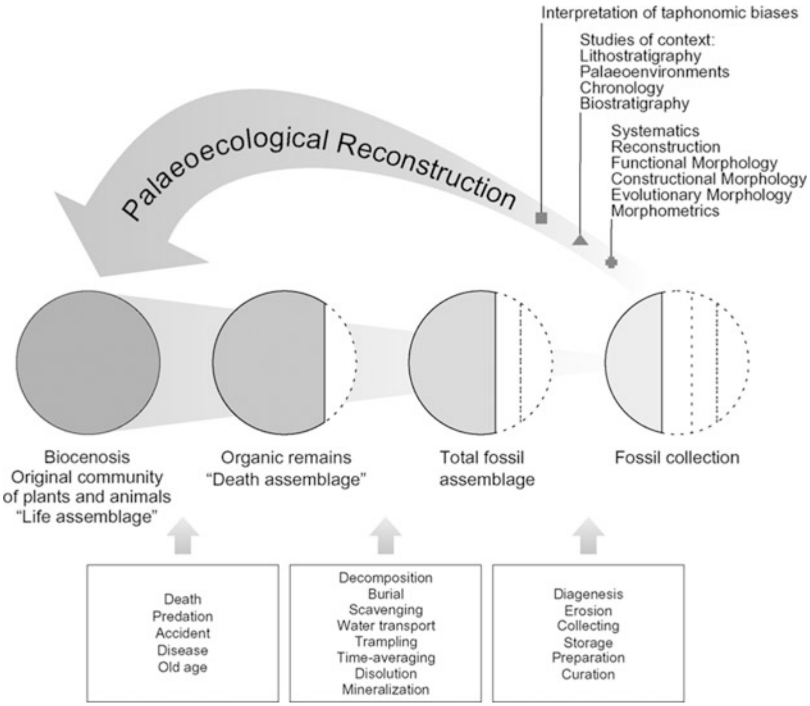


Fig. 10 The differences between life, death, and fossil assemblages related to taphonomic principles (Compiled from Lyman 1996 and Behrensmeyer 1992)

plants and developed terminal branch feeding on nectar and flowers (Bloch and Boyer 2002; Silcox et al., chapter "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence," Vol. 2). "Sussman has proposed that grasping extremities and nails on the digits evolved for eating fruit on terminal branches of angiosperms" (Sargis 2002, p. 1564). Presumably, our own ancestors began to walk upright long before they developed larger brains, since monotonous coverage of the landscape by tropical forest was beginning to fail due to climatic changes from warm and wet to arid and cool conditions in the Late Miocene (Vrba 1985; Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3; Wesselmann 1995; Bobe et al. 2002; Bobe and Behrensmeyer 2004). Sussman et al. (1985) and Rayner et al. (1993) suggested that, throughout the Pliocene, australopithecines showed arboreal and bipedal tendencies in a mosaic-like habitat that was marked by significant patches of subtropical forest, large areas of grassland, and savanna of all kinds. "Upright posture, large brain, tool making, and other hominin characters as adaptations to a savanna habitat must be rethought, at least in the case of *A. africanus*" (Rayner et al. 1993, p. 228; Rowan and Reed, chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1). In 2004 Schrenk et al. published a Pan-African so-called "open source" perspective suggesting that bipedal locomotion was developed several times at the margins of shrinking rainforest habitats during a global cooling trend in the Middle Miocene (Schrenk et al. 2004); for further discussions on the origins of bipedality, see Harcourt-Smith, chapter "▶ Origin of Bipedal Locomotion," Vol. 3 and Senut, chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). King and Bailey (2006, p. 282) state that the African Rift "... offers physical protection in the form of cliffs, lava flows and topographic enclosures, and hence small-scale topographic complexity in which a relatively defenceless species can find protection from predators." The authors expand their view and suppose that rift-like complexity could not only be found in areas where human evolution took place but along the dispersal routes of early *Homo* in and beyond Africa as well. Potts (2012, p. 163) concludes in a very clear review about environmental change as "first driver" in human prehistory that "Evolutionary processes favored any response that could enhance survival in a changing world. [...] This observation makes sense in light of the environmental instability that ancient human predecessors encountered." High plasticity and adaptability seem to be among the qualities that made *Homo*. Other factors, e.g., isolation, niche boundary shifts, and small population size, could also be a spur to evolutionary "innovations" in hominids (Wolpoff 1999; Henke and Rothe 2003). Just a few steps further in our evolutionary history, and in the debate concerning early *Homo* as well, there is a huge amount of different hypotheses that aim to link environmental constraints to specific adaptations and morphological transformations (Vrba, "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). Because of the insufficient preservation of plants in toto, caused by increased decomposition in aerobic and particularly tropical conditions, paleobotanists rely heavily on pollen, spore, and phytolith analyses (Jolly et al. 1998; Elenga et al. 2000; African Pollen Database). However, such things can be dispersed well away from their original habitat through wind and water (Andrews 1992). Density and distribution of these palynological units in sediment layers give us an idea about the allocation of specific plant families, spatial scales of retraction or expansion, and potential plant food proposed. For example, isotopic data on hominin diets have shown an involvement with C_4 grass – foods (Lee-Thorp and Sponheimer, chapter "▶ Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction," Vol. 1 and Sponheimer and Lee-Thorp, chapter "▶ Hominin Paleodiets: The Contribution of Stable Isotopes," Vol. 1). Large herbivores (e.g., gramineous, foliaceous) are bound to the availability, dispersal, and capacity of particular plants; subsequently, hypotheses about migrations of herds and "predator–prey" relationships between carnivores and early hominins may, respectively, achieve wider temporal and spatial scales. Bovids are the most common faunal element at most Neogene hominid fossil localities and are often used as indicators to understand Plio-Pleistocene hominid ecological and behavioral changes (Vrba 1995; Kappelmann et al. 1997). Besides, the strong interrelations between fossil species, phytogeography, climate, biogeography, and faunal conditions may lead to improved recognitions of "turnover pulses" in ecological networks and reflect the importance of environmental changes on faunal adaptation, selection, and evolution (Foley 1978, 1994, 1995, 1999; Potts 1998a, b; Lahr and Foley 1998; O'Brien and Peters 1999; Owen-Smith 1999; Vrba 1995, 1999; Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 1; deMenocal 2004; Hernández Fernández and Vrba 2006).

Syntheses

Modifying Dobzhansky's credo (1973) we state that *Nothing in evolution makes sense except in the light of ecology*. Corresponding to this "ecolution", we try to depict cross sections in three-time horizons (early-middle-late) of hominid evolution from ca. 7 Ma until today (Fig. 11). This should provide a basis for understanding how many different viewpoints have to be captured when looking at a complex process like hominoid and hominid evolution. It does not claim to circumscribe all factors in all periods; it can only provide insights and surely leaves many perspectives unseen.

But is there an "ideal" environment that can be hypothesized for the evolution of African hominids? This and other questions are discussed in this section. Two different kinds of hypotheses can be discerned: (1) the habitat-specific and (2) the variability-selection hypothesis. The former considers faunal adaptations to a specific environment, while the latter emphasizes the importance of climatic instability as a trigger for adaptive changes.

Modern interpretations support a step-by-step development of drier, cooler, and more open conditions since the Late Miocene. Both the influence of an arid-adapted fauna on early hominid evolution at the mid-Pliocene (near 3.2–2.6 Ma) and the aridification shift (Bonnefille 1983; deMenocal 1995; Dupont and Leroy 1995) are viewed as catalysts for human evolution.

Vrba et al. (1980, 1995, 1998; Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3) are prominent advocates of the turnover-pulse hypothesis that derives from the habitat-specific hypothesis, itself a variation of the savanna hypothesis. Fundamental shifts in African climate – 2.8, 1.8, and 1.0 Ma – initiated the so-called "turnovers." These turnovers are focused bursts of biotic change. For example, between 3.0 and 2.5 Myr, many first appearances were of grazing species. This pattern links aridity and expanding grasslands to faunal changes (Vrba 1980; Bobe and Eck 2001). Graphically, the pulses are defined via clustering. Authors, such as Behrensmeyer et al. (1997) or Werdelin and Lewis (2001), do not, however, support this important view of climate-hominid evolution interaction.

To make things more complicated, bipedality may have evolved in forest or woodland habitats, not savanna (Rayner et al. 1993; Wood and Harrison 2011); and maybe it was developed even in non-hominin primates like *Oreopithecus* (Rook et al. 1999). As concerns the evolution of early tool-making hominids, mosaic zones of grass- and woodland may have stimulated our evolution (Blumenschine 1986).

On the other hand, the *variability-selection hypothesis* advocates the importance of climatic instability for introducing (1) genetic plurality, (2) natural selection, and (3) faunal innovations. Potts (1998b) suggested that many of the largest African faunal evolution events occurred when there were increases in the amplitudes of paleoclimatic variability (such as modifications in the durations and amplitudes of orbital-scale wet-dry amplitudes). Potts' (1998b, p. 82) view stresses the inconsistency of selection over long time spans and "thus departs from the prevailing

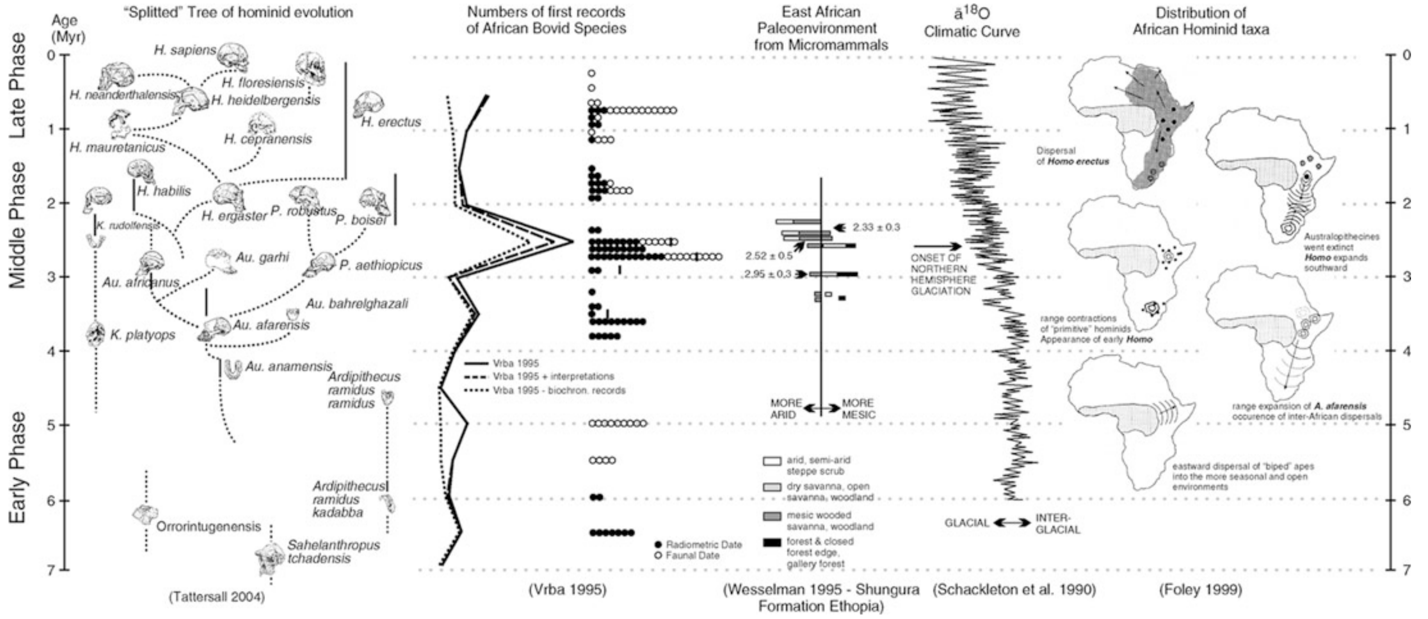


Fig. 11 (continued)

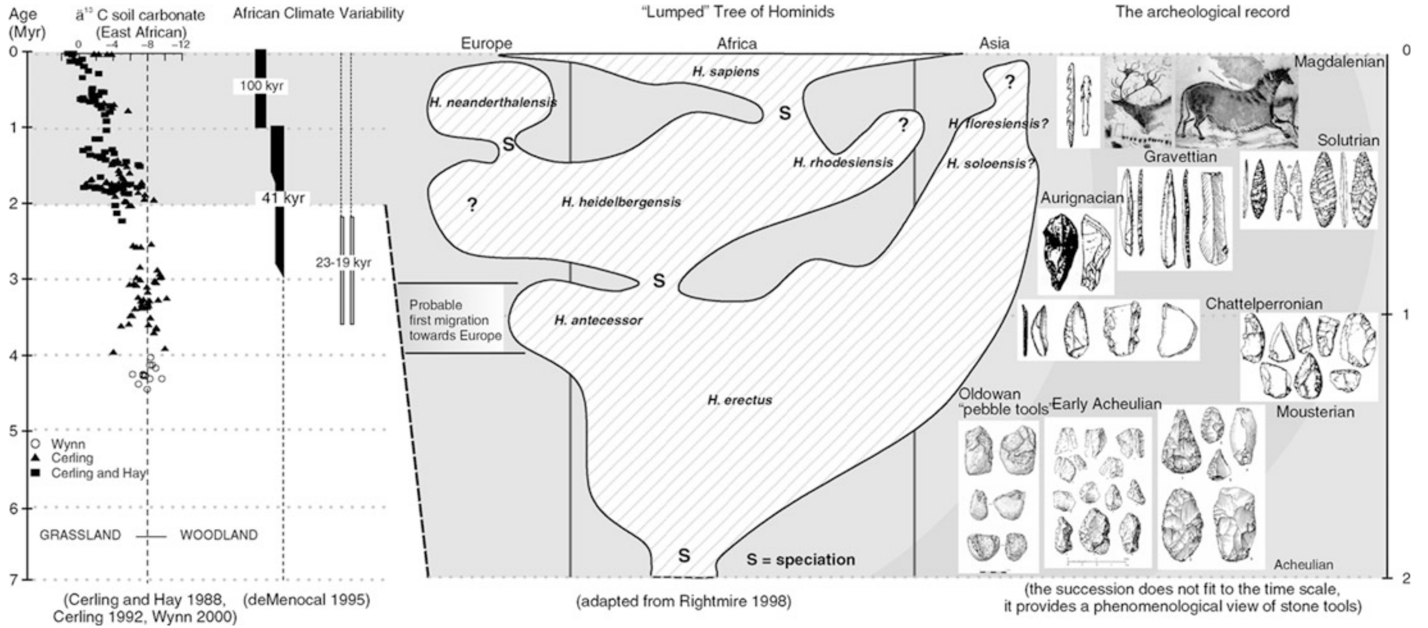


Fig. 11 Summary diagrams of paleoenvironmental data and hominid evolution, compiled from different authors. There is a clear linkage between hominid evolution, macro- and micromammal report, climatic changes, stable isotope data, and dispersals within and out of Africa. Seemingly, colder and more arid conditions combined with adaptational changes among hominids initiated several processes that led to the currently accepted patterns of biogeographical processes in hominid evolution. *Homo erectus* was the first hominin species to spread into the Old World. The taxonomic relationship between late hominin species is by no means completed. The evolution of stone tools comprises the last 2 Myr and leads to an explosion of artistic expression ca. 18 ka

paradigm of adaptive evolution via long-term directional selection." As many biologists (e. g., Sahney et al. 2010) assume a close match between an organism and its specific environment (that can be confirmed for organisms that are habitat specialists), the variability-selection model proposes that lineages experience factors over time that disrupt close connections to any specific environment – a decoupling mechanism that separates the organism from any environmental state.

Early Phase: Forerunners Among Miocene Primates

In the Late Miocene (23.8–5.3 Ma), the hominoids, including Hylobatidae and Hominidae [Ponginae/orangutans and Homininae/African great apes and *Homo*; sensu Groves (2001)], had reached their greatest abundance and diversity, and with little doubt human origins lie somewhere within this group (Conroy 1997). Niches now occupied by cercopithecoids were additionally exploited by hominoids in Africa (Fleagle 1999). The fossil records of the Early, Middle, and Late Miocene are fairly good and include Proconsulidae and Oreopithecidae as well (Godinot, chapter "▶ Fossil Record of the Primates from the Paleocene to the Oligocene"; Begun, chapter "▶ Fossil Record of Miocene Hominoids," Vol. 2; Rasmussen 2007). However, the search for the root of hominid evolution and additionally for "... the identification of hominoids among the various genera and species of fossil apes from that epoch has proved a fruitless exercise thus far" (Fleagle 1999, p. 483). Some propose *Dryopithecus* as a possible predecessor of the clade that includes great apes and humans; others suppose *Ouranopithecus* to be directly ancestral to later humans. The earliest fossils that are proposed as being probable hominid ancestors are two species of the genus *Ardipithecus* (*ramidus*/*kadabba*) 5.2–4.4 Ma from Ethiopia (White et al. 1994, 2009; Haile-Selassie 2001), *Orrorin tugenensis* ~ 6 Ma from Kenya (Senut et al. 2001), and *Sahelanthropus tchadensis* 6–7 Ma from Chad (Brunet et al. 2002). All these specimens were found in the last 20 years, probably because excavation campaigns were targeted toward the "roots' of hominids and the divergence point between apes and hominids, respectively. There is much debate about the "ape-or-human" status, the morphological features, the selection pressures, and the changes that have to be carried out on the tree of human evolution (Gibbons 2002), and of special interest here are the ecological circumstances around 7–4 Ma that these species were confronted by.

Ardipithecus is the name given to 5.8–4.4-Myr-old fossils from the Middle Awash area of Ethiopia. Haile-Selassie (2001, p. 178) declared *Ardipithecus* to be the genus that "... postdated the divergence of lineages leading to modern chimpanzees and humans." The fossils are associated with a relatively wet and wooded paleoenvironment (Haile-Selassie 2001; WoldeGabriel et al. 2001). WoldeGabriel et al. (2001, p. 175) suggested that similar habitats were found in the case of *Orrorin* (see later) and therefore that "... these findings require fundamental reassessment of models that invoke a significant role for global climatic change and/or savanna habitat in the origin of hominids." Associated vertebrate fossil assemblages indicate woodland/forest habitats and small areas of open grassland around lake margins. Among the micromammals the rarity of lagomorphs shows that open grasslands are not well sampled in the habitat of *Ardipithecus*. Moreover, closed wooded environments, where fossils are less likely to be preserved, may explain the low numbers of hominoid/hominid fossils in the Late Miocene. An eleven-paper publication in 2009 by an international team on *Ardipithecus ramidus* remains, including 110 fossil specimens and “Ardi,” a partial female skeleton comparable to the remains of “Lucy,” draws the following picture: this extinct 4.4-Myr-old species was a small-sized arboreal climber (without specializations for knuckle walking and suspension) in a tree-dominated habitat that had a nonspecialized “soft” C_3-food diet, showed minimal social aggression (reduced premolar/canine complex), and walked terrestrially as a facultative biped in a more primitive mode than *Australopithecus*. The unique compilation of traits in *Ardipithecus ramidus* perhaps helps us to develop a picture of the last common ancestor of humans and great apes. Thus, the authors concluded that a chimpanzee-like forerunner is unlikely (Science-Extra 2009).

East African *Orrorin* seems to fall somewhere between the African great apes and humans and thus “. . . accords with the East Side Story proposed by Coppens” (Senut et al. 2001, p. 142). The “East Side Story” is a construct that invokes the geomorphologically induced allopatric development of African great apes and hominids (~8 Ma) in the placement of the cradle of mankind in eastern Africa between the Great Rift Valley and the Indian Ocean (Coppens 1987, 1999; deMenocal 2004). A general trend of worldwide cooling, the extensive increase of grassland, and the retraction of tropical forests, rainforests, and wooded savannahs are perceptible ~8 Ma. At the same time, a rifting process and an uplifting of the western rift shoulder led to the appearance of a topographic borderline that placed them in the more and more arid eastern part in the rain shadow of the wetter western part (Pickford 1990). This eastern “isolation” for several million years might have been behind endemic peripatric genetic drifts and consequently the origin of hominid features (Coppens 1999). After analyzing and interpreting post-cranial morphological features, Pickford et al. (2002) conclude that *Orrorin* was a habitual biped with the ability to climb trees, and they found several apomorphic characters shared with australopithecines and *Homo* but none with *Pan* or *Gorilla* (Senut, chapter “▶ The Miocene Hominoids and the Earliest Putative Hominids,” Vol. 3). The habitat of *Orrorin* was reconstructed, from faunal remains and geological analyses of the Late Miocene Lukeino Formation in the Tugen Hills of Kenya, as a mosaic of open woodland and forests around a lake. *Orrorin* seems to be a representative of a typical “edge species” that lived on the frontier between environmental units (Sussman and Hart, chapter “▶ Modeling the Past: The Primatological Approach,” Vol. 1). Associated faunal remains stem from colobines, carnivores, and ungulates (Pickford and Senut 2001). However, the allopatric “East Side Story” is challenged by *Sahelanthropus tchadensis* – a 6–7-Myr-old hominin from western Africa.

S. tchadensis was found in Central Africa, in the western Djurab desert of Chad (Brunet et al. 2002). The locality is interesting because it lies far west to the Rift. Following the discovery of *A. bahrelghazali* in 1995, there was no further evidence for a western dispersal of hominids (Brunet et al. 1995) until *Sahelanthropus*, whose ecological circumstances are remarkable insofar as they are similar to those of the eastern fossil sites. This raises the possibility of analogizing evolutionary constraints for hominids in the eastern and western different areas. Vignaud et al. (2002) suggested that *Sahelanthropus* lived close to a vast lake with swamp areas and rivers (inferred from fish and amphibious forms) and not far from a sandy desert. As deduced from basicranial and facial structures, Brunet et al. (2002, p. 150) concluded that there are clear similarities between *Sahelanthropus* and "... later fossil hominids that were clearly bipedal." The faunal record shows animals associated with a mosaic landscape with lacustrine gallery forest, open grassland, and savanna (primates, rodents, equids, bovids, and carnivores). All of these observations led Brunet and colleagues to arrive at the conclusion that *Sahelanthropus* lived in a more mosaic-like habitat than *Ardipithecus*, *Orrorin*, and the australopiths (Blondel et al. 2010; Strait et al., chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3 and Rown and Reed, chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 3).

Still, all three new genera are represented by little fossil evidence and lack intraspecific comparisons, limiting inferences facilitating taxonomic placement of these fossils into the ape or the human lineages (Brunet et al. 2002; Wolpoff et al. 2002; Wood 2002; Senut, chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). In addition, for understanding the "start-up" of humanization, we also need to identify the selection pressures that triggered the evolution of bipedality and dental adaptations relating to dietary behavior shifts in changing habitats. Meanwhile, even the consensus from fossil and molecular evidence, that the human lineage diverged from that of the chimpanzees between ~6 and 8 Ma, is uncertain caused by the inconsistent calibration of the molecular clock we use as our "rearview mirror" (Stauffer et al. 2001; Gibbons 2012). Besides this, many questions linger pertaining both to the taxonomic classification of these "ape men" (Begun 2004) and the reconstruction of the paleoenvironments they lived in. "The solution is in the mantra of all paleontologists: We need more fossils!" (Begun 2004, p. 1480; Menke, "▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology," Vol. 1).

Middle Phase: "Chewer" and "Thinker"

Around 2.4–2.0 Ma, the genus *Homo* first appears in the fossil record of Africa. Its definition and the establishment of a hypodigm have given rise to a labyrinth of ideas and approaches about the number of species involved (Foley 1991; Tattersall 1992; Collard and Wood, chapter "▶ Defining the Genus *Homo*," Vol. 3), morphological variability, distinctions from the australopiths, and phylogenetic relationships. Recently, the bush of hominid evolution and especially the split between *Australopithecus* and *Homo* were altered by the 1.95–1.78-Myr-"young" remains of *Australopithecus sediba* found in the Malapa cave in South Africa in 2010. Because its cranial and postcranial features showed a mosaic of primitive (australopith) and derived (*Homo*) features, *A. sediba* was identified as a transitional species and hence a potential forerunner of early *Homo*. Once more another possible ancestor of *Homo* had been found in the australopith branch (Berger et al. 2010). As might be expected, there are other ideas: (1) *A. sediba* is only a late version of *A. africanus* (Tim White and Ron Clarke in Balter 2010); (2) *A. sediba* is an early *Homo* (Donald Johanson cited by Wong 2010); and (3) *A. sediba* is a late form of australopiths that lived at the same time as early *Homo*, leaving taxonomic questions and coming back to paleoecology. Analyzing *A. sediba's* dental phytoliths, stable carbon isotopes, and dental microwear, Henry et al. (2012) infer a C_3-plant diet in a gallery forest like biome with C_4-grassland and woodland in the vicinity. The home ranges of *A. sediba* could thus have been large and comparable to that of modern savanna chimpanzees striving for C_3-fruits. The upper limb of *A. sediba* shows ape-like climbing and suspensory abilities than manipulation skills like in *Homo* (Churchill et al. 2013). Albeit the lower limb clearly shows the capability for bipedal walking, the gait mechanics seem to be different from what we knew previously in *Australopithecus*. DeSilva et al. (2013, p. 1232999-1) conclude that "… there may have been several forms of bipedalism during the Plio-Pleistocene." The crucial questions regarding the borderline between *Australopithecus* and *Homo*, and exactly which forms gave rise to genus *Homo* and which ones originated the "robust" lineage around 2.5 Ma, are still unanswered. From the ecological point of view, the crucial question is: "*Why did these two lineages split off*?" In our opinion the base of all "changes-driven" suggestions is the innate skill of organisms to adapt to environmental changes. Vrba (1988) provides an overview of general hypotheses that relate environmental changes to biotic evolution and thus provides a basis to speculate about divergence processes (Table 6).

Late Pliocene and Early Pleistocene strata contain a number of hominid fossils that obviously belonged to different morphotypes and ways of living. On the one hand, there are robust forms with large faces, huge supraorbital structures, small brains, and enormous masticatory capacities; on the other hand there have been forms with small faces, larger brains, reduced supraorbital features, and reduced size of upper and lower jaws. The latter are associated with the first 2.4-Ma-old lithic tools ("pebble tools" and "choppers") as attributed to the Oldowan industry and "handy man" *H. habilis*. It remains doubtful that australopithecines maintained the kind of Osteodontokeratic culture (bone, teeth, and horn) that Raymond Dart (1957) proposed.

The focus here lies on the outstanding trends that divide two temporally sympatric genera and morphological/evolutionary "lineages": *Paranthropus* and early *Homo*. The different ecological niches that could have been occupied by the species of both genera are limited by their basic needs as (1) large mammals, (2) terrestrial primates, (3) dwellers of tropical gallery forests/open savanna – or grassland – habitats, (4) interspecific competitors, and (5) K-strategists (Foley 1978; Henke and Rothe 1994, 1999). When reflecting on the possibilities of coping with the environment and niche separation as well as niche expansion, the encompassment of all kinds of "internal" influences like body size, population dynamics, abilities of locomotion and "thinking," life-history strategies, behavior, and social system is

Table 6 Hypotheses of how environmental changes relate to biotic evolution

Hypothesis	Description
Refugial vs. biotidal areas	Environmental changes affect two basic kinds of geographical areas differently: the biome resists in a refugium, whereas it does not in a biotidal area. Refugia are characterized by the persistence of dominant taxa (new species within these taxa may be added); in contrast, biotidal areas are shaped by the temporary appearance and disappearance of dominant taxa
Turnover pulse (local/ widespread)	Physical environmental change is required to initiate most speciations, extinctions, and distribution drift. Thus, most lineage turnover has occurred in pulses, near synchronous across diverse groups of organisms. Changes could either be widespread with independent evidence of environmental change or they are mostly local and form a largely random frequency distribution against time
Coordinated stasis hypothesis	Organismic interactions are the reason for evolutionary stasis in a community. Only radical physical changes can detach the coevolutionary bonds between the life-forms, comparable to the turnover-pulse hypothesis
Climatic/tectonic initiating cause	A particular environmental cause of turnover was global, or at least widespread, climatic change. Alternatively, the cause could be tectonic, and thus turnover signature is appropriately geographically restricted
Variability-selection hypothesis	Advocates the importance of environmental variability for introducing (1) genetic plurality, (2) natural selection, and (3) faunal innovations

Compiled after Vrba (1988), Potts (1998); see also Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3

required. Furthermore, the roles of "external" factors such as climate, biogeography, sympatric species, and predator–prey relationships have to be taken into account (Foley 1978).

About 2.0 Ma, several kinds of hominids are found in northwestern Kenya and south Ethiopia around Lake Turkana (Tattersall 2002): *Paranthropus boisei*, *P.* (*Australopithecus*) *aethiopicus*, *H.* (*Kenyanthropus*) *rudolfensis*, *H.* (*Australopithecus*) *habilis*, *H. erectus* (*ergaster*); the genera and species names in parentheses indicate that the debate about their taxonomic status is still in progress. The Turkana Basin (Fig. 3), situated in the Great Rift Valley from southern Ethiopia into northern Kenya, covers an area of about 3,600 km^2 and represents one of the richest fossiliferous areas in Africa. An exceptional breadth of "mosaic-like" geological and environmental diversity has been investigated by the Koobi Fora Research Project. It reaches from the lacustrine/fluvial sediments of the Omo River channel, with gallery forests and swamps, across thorn bush and grassy floodplains strongly influenced by seasonal flooding, to the basin margins with an arid climate and totally different sedimentation regimes (kfpr.com/prehistory_of_koobi_fora). The geological record provides volcanic tephra layers, amenable to chronometric dating, that are associated with unusually well-preserved fossils. The faunal record has a nearly gapless temporal as well as a lateral component, making it possible to reconstruct paleohabitats over large areas. The archaeological remains include Oldowan, Karari, and Acheulean tools that complement the evidence of the fossil hominins.

The Omo basin sediments, fossils, and pollens provide a wealth of information about the ecological circumstances and the temporal distribution of hominids in this region. *P. boisei* and *P. aethiopicus* are strongly adapted to drier conditions in savanna habitats with gallery forests or patchy wooden refugia. Craniodental morphology and especially microdental analyses suggest an exclusively low-quality herbivorous subsistence with sometimes coarse gramineous parts, dependent on the availability of food in a highly variable seasonal environment that is characterized by both copiousness and scarcity (Rak 1983; Foley 1987; Kay and Grine 1988; Henke and Rothe 1999). In contrast, gracile australopithecines seem to have preferred more humid habitats with large spots of forest (Coppens 2002) and were able to accommodate to substantial environmental variability and dietary shifts (Teaford and Ungar 2000; Bonnefille et al. 2004).

The most widely studied *habitat-specific hypothesis* is the savanna hypothesis. Dart (1925) already used the open savanna model as a tool to explain larger brains and bipedality in early *Homo*. This concept plausible prima facie was not confirmed by the data collected (Leakey and Hay 1979; Cerling 1992; Cerling and Hay 1988; Senut et al. 2001): bipedalism was apparently established millions of years *before* the savanna grassland expansion. Early *Homo* lived in fairly open, arid habitats, used an enlarged spectrum of food resources, and is best characterized as an opportunistic and omnivorous forager. Basic sustenance was surely provided by plant food, but the use of tools made accessible difficult-to-reach high-energy sources like edaphic storage organs (tubers and roots) (Laden and Wrangham 2005) and meat from scavenging complemented their diet (Foley 1987; Blumenschine et al. 1994). This latter is important when looking at coevolutionary processes and sympatric interdependencies between early *Homo*, herbivores, and carnivores (Turner 1984; Lewis 1997; Brantingham 1998). High-energy-density diets and unstructured feeding patterns (originated by the seasonal availability) still characterize present-day human eating behaviors, although today's nutrition is largely uncoupled from seasonal cycles (Ulijaszek 2002). Hunting, as Lee and DeVore (1968) suggested, is widely accepted as unlikely in early *Homo*; it seems that the conception of a klepto-parasite seems to characterize the real natural situation best. Comparative primatological studies of chimpanzee populations and analyses of behavioral ecology and nutrition strategies in current African hunter-gatherer tribes (Lupo 2002; Marlowe 2005) support these assumptions. Vrba (1988, p. 422) stated that "… in some respects the *Homo* lineage evolved toward a greater ecological generalization, while in contrast the 'robust' lineage(s) became more specialized on resources prevalent in more open environments."

In the Middle and Late Pleistocene, the diversity of hominids decreased drastically; the "robust" australopithecines became extinct, maybe because they were too specialized and could not adapt to the changing environmental conditions (Klein 1988); and *Homo* constituted the only remaining genus in the bottleneck of hominid evolution. The questions of how and why that happened and what processes were involved are manifold (Henke and Rothe 1999; Tattersall 2002; Rightmire 1998, chapter "▶ Later Middle Pleistocene *Homo*," Vol. 3).

Late Phase: Neanderthals and Colonizers

As one of the most discussed topics in human evolution, the Neanderthal enigma is a prominent "problem" of the late phase. d'Errico and Sánchez Goñi (2003) investigated the millennial-scale climatic variability of OIS3 in the context of Neanderthal extinction. To the extent that population models seek climate as a triggering factor for the colonization of Europe by anatomically modern humans and the Neanderthal extinction, they appear to be highly contradictory due to (1) the lack of terrestrial continuous and well-dated paleoclimatic sequences, (2) the uncertainties in the dating methods, and (3) the doubts about the cultural attribution of archaeological layers. These authors therefore reviewed the paleoclimatic OIS3 evidence from Iberia and found a fragmentary, low-resolution, and poorly interpreted record. d'Errico and Sánchez Goñi (2003) concluded that Aurignacian moderns colonized the north of Iberia and France at the onset of the H4 event. They based their results on a correlation between archaeological data from western Europe and from two images pollen-rich deep-sea cores. Their scenario favors Neanderthal populations existing in desert-steppe-like environments (made up of *Artemisia*, Chenopodiaceae, and *Ephedra* which characterize the H4 of this area), while the Aurignacian moderns were probably not interested in colonizing these arid Mediterranean biotopes. Anatomically modern humans did this only after the H4 event.

However, Finlayson et al. (2004) pointed out problems with this scenario. They admit that d'Errico and Sánchez Goñi's (2003) paper is very useful in reinforcing the data showing that climatic events worldwide became increasingly unstable during OIS3, but as inferred by Finlayson et al. (2004, p. 1208), there are problems of cause and effect: "We suggest that this is a spurious correlation, and that what is being observed is two populations responding to the same variable (or variables) in opposite directions. Since no direct proof of cause and effect between Aurignacians and Neanderthals is advanced, this must remain the most parsimonious explanation." Finally, they interpret d'Errico and Sánchez Goñi's (2003) data in the opposite way by concluding that the available information points to climate instability fragmenting Neanderthal populations and emphasizing that not a single piece of evidence exists to demonstrate competition between Moderns and Neanderthals.

Further questions that have to be answered when discussing anatomically modern humans in Eurasia, Australasia, and the New World are the following: *Why and when did the expansion happen*? *Who and how many participated and where did they arrive*? Fig. 12 provides an overview of potential migration waves and the time they probably took place. One consensus seems to crystallize from the fossil record: equipped with a stature shape and size near to ours (Turkana boy from Nariokotome), a large brain, and increased mobility; able to handle hunting

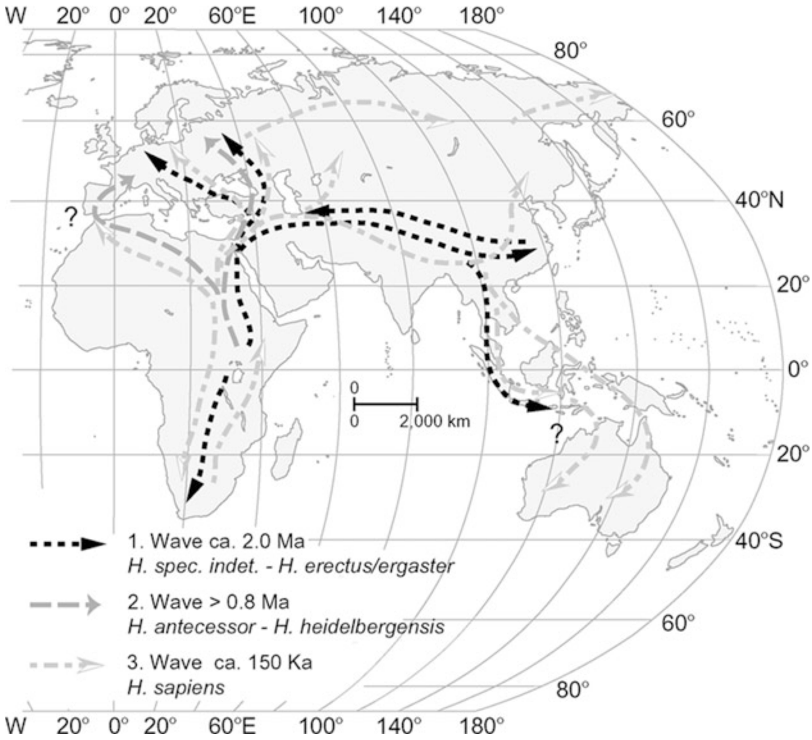


Fig. 12 Potential migration waves and migration periods of archaic *Homo* populations "Out of Africa" assumed by several paleoanthropologists (After Henke 2004)

weapons (400-ka-old spears of Schöningen/Germany) as well as fire; and being provided with a significant curiosity, *H. erectus* (*H. ergaster*) migrated far from the continent of its birth at around 1.8 Ma (Dmanisi fossils) (Gabunia et al. 2001) and conquered the Old World. Thenceforward, there are diverse models/hypotheses that try to explain dispersal patterns over the last 1.5 Myr of human evolution. The recent African origin model (RAO) holds that the biocultural transition from late archaic *H. sapiens* to anatomically modern humans was restricted to Africa, with subsequent dispersion and replacement of *H. erectus* ca. 200 ka. Another hypothesis assumes an anagenetic transition from the early hominins to *H. erectus* (earlier than 1.5 Ma), followed by dispersal. In the view of Templeton (2002), a second and a third expansion (Out of Africa "again and again") shaped the modern human gene pool. The assumption that *H. sapiens* developed independently and in parallel in several regions of the world is mainly based on Asian fossils (e.g., Zhoukoudian, upper cave) and is summarized as the "Multiregional Continuity Model," or the polyphyletic hypothesis, with gene flow maintaining some genetic homogeneity (Wolpoff 1999, 2002). The "mostly Out-of-Africa hypothesis" (Relethford 1998, 2001) is a combination of the African replacement model with the multiregional model. All these hypotheses involve questions of whether migrating hominins replaced local populations, or interbred (for further discussions, see also Bräuer, "▶ Origin of Modern Humans," Vol. 3).

Referring to the questions we formulated at the beginning of this section, we want to add a third one: *how did hominins migrate from Africa*? (Henke and Hardt 2011). In the early phase, hominids seem to have been restricted to certain African habitats (although there were relatively large numbers of "intra-African" dispersals Strait and Wood 1999); this restriction lapsed through the Pleistocene, and hominids seemed to become more eurytopic and thus became able to tolerate a wider range of conditions (Foley 1978; Vrba 1995, 1999; Lahr and Foley 1998). It is possible to see an ecological patterning in the colonization of temperate regions even when looking at the range of other species (mostly large mammals) that spread out of Africa alongside the hominids (Turner 1984; Lewis 1997; Brantingham 1998; Strait and Wood 1999). Certain characteristics of large mammals provide the capacity to exploit new environments, including (1) large body size, (2) carnivorous behavior, and (3) sociality in larger groups. Hence, scientists have to think about the general principles that encourage zoogeographic mobility (Foley 1987; Henke and Rothe 1999):

- *Carnivores* are more *eurytopic* than herbivores. Meat requires less specialized and locally restricted adaptations than plants, thus carnivores are expected to migrate faster than herbivores, which are restricted to specific plants in a specific area.
- *Exogeny*: the attribute of an organism to forage across a variety of niches, giving it higher tolerance, less specialization, increased interspecific competition.
- *Environmental physiology*: increasing body size enhances the energetic situation of an organism in terms of the relation between body weight and surface (Bergmann's rule 1847; Aiello and Wells 2002). Consequently, larger mammals are able to cope more efficiently with temperate conditions. The extremities tend to be reduced in colder environments to diminish frostbite as seen in the distal limb segments of Neanderthals (Allen's rule 1906). "There is indeed some possibility that the increase in body size associated with *Homo erectus* [...] may have at least contributed to the success of human geographical spread" (Foley 1987, p. 268).

Additionally, home range size and diet quality seem to be closely related to initial dispersals from Africa (Antón et al. 2002). Although these principles are able to account for the expansion of early hominins, certain problems related to surviving high-latitude habitats remain: (1) resource availability is highly seasonal and (2) the annual variation in day length shortens the time for foraging and other activities in winter. Favored strategies here are the extraction of resources yielding high returns and an increase in the efficiency with which resources are extracted. The former is linked to an increase in carnivory and high-energy food and the latter to increasing predatory efficiency and, especially in hominins, improved tool manufacturing and using. Additionally, producing complex and efficient stone tools demands advanced cognitive competence and accordingly constitutes an interaction between encephalization and culture (Klein 2000; Wynn 2002; Osvath and Gärdenfors 2005; Biagi, chapter "▶ Modeling the Past: The Paleoethnological Approach," Vol. 1 and Toth and Schick, chapter "▶ Overview of Paleolithic Archaeology," Vol. 3). Most likely, habitat structure and resource types were the driving forces that mainly influenced dispersals and the sequence of habitat colonization by hominids (Foley 1987).

Conclusion

Human evolution is not a "Sonderweg" (exceptional way); it strictly follows the rules of evolutionary biology and neither constitutes a special case nor determines the terminal branch end in the Tree of Life, let alone creation's crowning glory (Foley 1978, 2002). It is just the story of balanced interrelationships between environment and large mammalian genera possessing preadaptations that facilitated coping with the conditions during a specific time span. Corresponding to Foley (2002), the following key events altered the direction of radiations and dispersals in the hominid lineage:

1. *Invasion* of Africa from Asia of an ancestral lineage of Miocene primates and the outcome of African apes and potential "hominids" *Ardipithecus*, *Orrorin*, and *Sahelanthropus*.
2. *Bipedal adaptations* in australopithecines living in tree-dominated grassland-woodland mosaic habitats probably in dense gallery forest biomes and/or at the margin of the shrinking central African rainforest (taxa: *A. anamensis*, *A. afarensis*, *A. africanus*, *A. garhi*, *A. bahrelghazali*, *A. sediba*) in the Pliocene with nearly Pan-African dispersals.
3. *Megadonty and masticatory apparatus increase* as adaptation to low-quality nutrition in a mosaic-like environment in the "robust" australopithecines (taxa: *P.* (*A.*) *aethiopicus*, *P.* (*A.*) *boisei*, *P.* (*A.*) *robustus*) during the latest Pliocene and Early Pleistocene leading to an extinct backside branch.
4. *Origin and radiation of earliest Homo* is the most intriguing event of all because the phylogenetic position of the scarce fossils is extremely uncertain and variations within the group are extensive (taxa: *A.* (*H.*) *sediba*, *Kenyanthropus platyops*, *H.* (*K.*) *rudolfensis*, *H. habilis*). Nevertheless, there is a clear trend toward *brain size increase*.
5. The *diversification and dispersal* of *Homo* 1.75 Ma (taxa: *H. erectus*, *H. ergaster*) and a second radiation of later forms of *Homo* 0.5 Ma (*H. heidelbergensis*), bound to several changes in dental/cranial morphology and behavior (*carnivory*, *hunting*, *tradigenesis*), the development of technologies (*stone tools*), and the usage of *fire*.
6. Enhanced neural capabilities and improvement of lithic and hunting technologies (e.g., projectiles) in the context of interglacial/glacial cycles may have led to repeated dispersals following each other with the outcome of *H. neanderthalensis* and *H. sapiens*.

7. *Symbolic thought* (Henke in press) combined with *language* and the opening of new resources (e.g., aquatic food) characterizes the radiation and global colonization of *H. sapiens* in the last 100 kyr ago. Why and how the Neanderthals became extinct is still a matter of debate.
8. Recently, humans seem to have nearly *detached themselves from selection pressures* (except regarding their own species and some kinds of pathogens). Meanwhile, *Homo* is the large mammal species with the most individuals – there are seven billions of us now. This, however, brings with it great responsibility to safeguard "System Earth" in order to afford further evolutionary development in global ecosystems. The sheer mass of *Homo sapiens* is causing systemic changes in every sphere of the planet that are faster than ever before in the Earth's history. We are now in the Anthropocene (Zalasiewicz et al. 2011). Or, as Potts put it (2012, p. 163): "The question remains as to how human societies in the future will apply their evolved adaptability in adjusting to the rapid changes we now create."

We would like to stress that primate and consequently hominid evolution is a complex process that has to be seen from different angles and needs all of the different scientific approaches currently available.

One question remains open: *Is paleoecology an adequate window on the past*? This is answered in the affirmative but, as in any other hypothesis-based scientific field, it is also realized that without paying attention to possible pitfalls and without interpreting the results in context, there is a danger of simply telling stories. Unfortunately, there are no "laws" in ecological science such as those that exist in chemistry and physics; there are merely a lot of hypotheses that have to be tested and one concept that is close to a "law": *natural selection* (Pianka 1983). Hence, we conclude that paleoecology – when conceived with care – is an important field of evolutionary biological, and especially paleoanthropological, research. When discussing hominid evolution, and consequently our own evolutionary history, the danger of storytelling is potentially higher because fossils are rare, sample biases are high, and not least because hypotheses always stand on shaky ground when the subject is ourselves (White 2000).

Actualism may be a path that leads to "true" inferences when ecological models and model organisms are selected carefully. For example, *Pan*, as our genetically closest relative, seems to be a good model from which to derive certain inferences, but as a restricted occupant of dense and humid forest habitats with significant morphological adaptations, it might not be the first choice for reconstructing the selective pressures that affected early humans living "on the edge" between open and closed habitats (see also Susman and Hart, chapter "▶ Modeling the Past: The Primatological Approach," Vol. 1).

It is obvious that paleoecology demands a multidisciplinary approach. However, nearly all researchers are specialized in their own "scientific niches" and struggle to keep and defend them. The great challenge ought to be the creation of a "scientific biocenosis" that helps us to understand evolutionary processes in terms of all the phenomena scientists are able to examine. The "scientific environment," however, is sometimes harsh, and chilly winds wave the banner of publication quantities and impact factors. There is hope that a high adaptational species – such as ourselves –could change and improve this "habitat" to enhance the "ecology" of pure science.

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Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

Alan Turner and Hannah O'Regan

Contents

Abstract

Human evolution may be usefully considered as part of the evolution of the larger mammalian fauna of the Tertiary and Quaternary periods. When viewed in this way, the dispersion of the hominins, and the questions of timings and directions, can be examined in the context of movements in other mammalian groups without being treated as special case with a unique set of causes. Earliest migrations by Primates into Africa during the Oligocene and Miocene were accompanied by numerous other taxa that were capable of crossing the closing gap between

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Alan Turner passed away in January 2012. This chapter has subsequently been updated by his co-author, but not rewritten.

A. Turner
Deceased. Formerly at School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK

H. O'Regan (✉)
Department of Archaeology, University of Nottingham, Nottingham, UK
e-mail: Hannah.O'Regan@nottingham.ac.uk

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continents. While the later evolution of the Hominidae may well have taken place in Africa, the dispersion patterns of the dryopithecine apes during the early Middle Miocene into Eurasia and then back into Africa toward the Late Miocene suggest a rather wider ancestry for humans and the living African apes. Earliest movements across the Gibraltar Straits during the Pliocene and Pleistocene can be ruled out for any terrestrial mammals, and while a Late Pliocene dispersal across the opening Bab el-Mandeb region of the southern Red Sea may have been possible, such a route appears an unlikely choice for a Pleistocene gateway leaving only the Levantine route across Sinai as a plausible way out of or into Africa.

Introduction

It is a commonplace observation that species of both plants and animals have patterns of distribution, and that everything is not found everywhere (Cox and Moore 2004). In many cases, such distributions can be explained by the presence of physical or biotic barriers such as mountains, deserts, or water and the absence of suitable foods, while some clearly owe much to modern human interference. But a species may not have always been where it is found now, while another may formerly have existed in areas from which it is now absent, so that many patterns reflect processes of movement that occurred from a few tens to thousands or millions of years ago. We live on a planet that has been constantly changing as the continents have shifted and climates have altered, and it is likely that many of the patterns we observe today have been affected by such events.

Change in zoogeography over geological time, and its relationship to tectonic and climatic events, is one of the things that the fossil record can bring to providing a bigger picture of the past, although pitfalls must be overcome in the process. Identification and dating must be accurate, and while presence is clear enough from the fossils, firm evidence for absence in a region may be rather more difficult to distinguish from simple failure to look in the right place or simply to find. But the fossil record is never as good as it will become, and synthesis cannot forever be delayed on the grounds that we do not yet have enough data. As time goes on, and more evidence accumulates from more and more sites, even absence may start to be seen as a real feature of the record and attempts at synthesis of zoogeographic patterns may legitimately be made (Turner and Wood 1993).

Paleoanthropology deals with the evolution of *Homo* and our close fossil relatives, the tribe Hominini or hominins, and may be extended, according to the interests of the enquirer, to include the evolution of the Hominoidea (the superfamily that includes lesser apes, great apes, and humans) or even more widely to other primates. In the case of the Hominoidea, one of the most important issues to understand is the question of dispersions, whether of the Primates into Africa in the first place or our closer hominin fossil relatives out of Africa in the later stages of their evolution. It could be argued that the dispersals of the Hominoidea are likely to be best understood within the context of dispersals in other elements of the mammalian fauna, and here this larger context is examined, beginning with a brief discussion of the initial movement of the Primates into Africa, followed by a review of the evidence for Miocene to Early Pleistocene distributions within Africa and between Africa and Eurasia.

Early Movements of Primates into Africa

Recent molecular analyses of DNA sequences suggest that a small number of mammalian orders (the elephants, hyraxes, tenrecs, aardvarks, elephant shrews, golden moles, and the aquatic manatees or sea cows) together compose a unique group, the Afrotheria, whose members share a restricted common ancestry (Tabuce et al. 2008). The fact that the closest (sister) group to these is likely to be the South American order Xenarthra (the sloths, anteaters, and armadillos) makes sense in terms of continental separations (Asher et al. 2009). A significant absence from the Afrotheria, however, is Primates, which seem to have evolved in the Northern Hemisphere (Fleagle 1999).

The Afrotheria owe their origins as a distinctive group to the fact that the continent was long isolated after the breakup of the southern landmass of Gondwana. Africa and the southern part of the Arabian Peninsula finally docked with the Eurasian plate in the Early Miocene, around 25–18 Ma, after a northward movement from the breakup estimated at around 14° of latitude (Rögl 1999). In the process of closing with Eurasia, the eastern arm of the Tethys seaway was closed, providing a land connection. At what precise point movements across the shortening gap between Africa and Eurasia became possible for terrestrial animals is unclear, but primates are known in some numbers from the Fayum deposits of Egypt between 37 and 30 Ma, with an earlier appearance between 52 and 46 Ma suggested by material from Algeria (Tabuce et al. 2009). The implication is that some form of island hopping across the shortening gap was possible as tectonic forces buckled the floor of the Tethys and produced a series of small and no doubt short-lived areas of dry land. Following the contact between Africa and Eurasia, a transgression of the Tethys Sea southward left Africa connected to Eurasia via the southernmost part of the Arabian Peninsula across what are now the Bab el-Mandeb Straits (Tchernov 1992). Much of the later Miocene movement of faunas into and out of Africa therefore probably took place across this region, although our knowledge of the Miocene mammalian fauna of Arabia is currently very poor (Whybrow and Clements 1999).

Those same enormous forces produced by the combined northward movement of Africa and India formed the mountain chains that run from southern Europe to the Himalayas. These include the Taurus and Zagros mountains of Turkey and Iran, which have combined with the frequently harsh conditions of the Arabian Peninsula to control movements into and out of Africa (Tchernov 1992) (see also later). Toward the end of the Miocene, during the Messinian salinity crisis, tectonic processes in the westernmost region closed the portal with the Atlantic and the Mediterranean began to dry up (Kirjksman et al. 1999). During the Early Pliocene, the Mediterranean refilled, while the Red Sea widened as the Arabian plate swung away and eventually broke the Bab el-Mandeb land bridge in the Late Pliocene, part of the eastern African rifting process that continues to the present day. Although some form of land bridge therefore existed between southern Spain and northern Africa during the Messinian (Gibert et al. 2013), there is no compelling evidence for one across the Gibraltar Straits since then. Most if not all subsequent mammalian movements between Africa and Eurasia during Plio-Pleistocene times are therefore likely to have been via the Levant and perhaps Arabia (see later).

The Eocene to Oligocene primates of the Fayum were already quite diverse and numerous genera have been recognized (Seiffert et al. 2010), but their relationships to modern primates have yet to be established. Such diversity points to a well-established presence at that point, but the subsequent record of monkeys is poor until well into the Miocene, when records recommence in the rich deposits of eastern Africa where numerous remains referred to the family Victoriapithecidae occur (Jablonski and Frost 2010). Primitive apes appear in the fossil record of Africa a little later than the monkeys, and there is a reasonably good record from Late Oligocene to mid-Miocene deposits. One of the oldest specimens comes from Lothidok Hill in northern Kenya, in deposits that may be as early as 27 Ma, while others are found at a range of Early Miocene sites in Uganda and Kenya such as Rusinga Island in what is now Lake Victoria, at Koru and at Songhor in deposits dated to the period 22–17 Ma (Andrews and Humphrey 1999). These animals, belonging to the genera *Proconsul*, *Rangwapithecus*, and *Nyanzapithecus* and varying from large monkey-like up to female gorilla-like in size, are placed in the separate family Proconsulidae and best characterized as "arboreal quadrupeds" (see Begun, chapter "▶ Fossil Record of Miocene Hominoids," Vol. 2).

More advanced apes appear in a further radiation in the period 17–12 Ma, and are referred to three superfamilies – the Dendropithecoidea (Family Dendropithecidae), Proconsuloidea (subfamilies Proconsulinae, Afropithecinae and Nyanzapithecinae), and the Hominoidea (subfamilies Kenyapithecinae and Homininae) (Harrison 2010). It is at this stage that primates appear to have moved back out of Africa. Although the Afropithecinae occur in Africa and Arabia, the Kenyapithecinae are known from Kenya but mostly occur in Turkey and southeastern Europe, while members of the Homininae (tribe Dryopithecini) are European in distribution (Begun 2009). In other words, the major known fossil distribution of the early Hominoidea is outside Africa. This early dispersion from Africa may have implications for our understanding of the later origins of the Homininae, the subfamily containing the African great apes and humans (see below).

The earliest movement of the Primates into Africa may have been "accompanied" by a dispersal of the archaic predator order Creodonta, since members of the family Hyaenodontidae also first appear in Early Eocene deposits there, but further contemporary incursions of other groups are not evident. A clearer pattern emerges at the time of full contact around 20 Ma, when other immigrants from Eurasia included the first perissodactyls in the form of early rhinos, and the bizarre-looking chalicotheres, with their horse-like heads and clawed feet. More artiodactyls also made their appearances, with the incursion of the giraffoid climactocerids and first antelopes as well as primitive pigs of the genus *Nguruwe*, which must have traversed the continent since they are known from Namibia and Kenya at around 17.5 Ma

(Turner and Antón 2004). More advanced cercopithecoid monkeys replaced the earlier primates, although in situ evolution is hard to distinguish from immigration. True Carnivora entered the continent with the first appearance of cats and the amphicyonid bear-dogs as well as of mustelids (Morales et al. 1998) and, at least in North Africa, of members of the extinct cat-like family Nimravidae, although the creodonts continued to prosper as the dominant meat eaters. In the other direction, the probable dispersion of dryopithecine apes was perhaps preceded by the appearance of anthracotheres in Europe and possibly accompanied by a dispersal of monkeys of the genus *Pliopithecus*, the creodont *Hyainailouros* (Agustí and Antón 2002) and the first movement of the proboscideans from Africa (Harzhauser et al. 2007). The latter consisted of movements not of elephants proper but of the four-tusked gomphotheres and the deinotheres, the latter marked by a single pair of tusks set in the lower jaw. The subsequent history of some of the various proboscidean genera during the Miocene and Pliocene suggests a good deal of interchange with Eurasia.

On a general note, the structure of the African Early Miocene guild of larger carnivores seems to have divided into flesh-eaters among the early cats, nimravids and perhaps smaller creodonts, and bone-crunchers among the amphicyonids and larger creodonts, and by the mid-Miocene, the complexity in the guild structure of carnivores was enormous. Such a guild points to an equivalent complexity in the ecological relationships of predators and prey in Africa at this early period. The ungulates do not look particularly well adapted for speed, while the predators do not look equipped to chase anything moving particularly fast. Dog-like animals, in the form of some of the smaller hyenas of the genera *Ictitherium*, *Hyaenictitherium*, *Lycyaena*, and *Hyaenictis*, only appear much later in the Miocene (see later) and in the absence of the true dogs of the family Canidae until later still in the Pliocene it is difficult to assess the extent to which pack hunting might have been possible (Turner and Antón 2004). The larger amphicyonids are unlikely to have operated cooperatively, and would probably have taken a mixture of carrion and hunted meat. Overall, the zoogeography that can be pieced together supports interpretations of the earlier to Middle Miocene vegetation of Africa as generally quite closed (Cerling 1992; Cerling et al. 1997). It might therefore be presumed that most of the primates at that time would have found food and refuge among the closed vegetation, and as such have been fairly safe from predation, but the latest work on material from Kenya suggests that Miocene primates were preyed upon by a variety of animals (Jenkins 2011).

Zoogeographic Evidence for the Origins of the Hominidae

Africa is usually taken to be the origin point of the human lineage, and so far as the later stages of the Pliocene and Pleistocene are concerned, this is generally accepted as true beyond reasonable doubt. Nevertheless some doubts about this matter have been raised in recent years – in particular regarding the origins of *Homo erectus* (White 1995; Dennell 2004) – and it would always be unwise to assume that there are no surprises left in the fossil record. However, as discussed above, the Primates themselves did not originate in Africa, and while emphasizing their incursion during the Early Eocene may seem like an academic nicety, it is worth stressing that the intermediate period of the mid- and later Miocene witnessed emigrations and perhaps also re-immigrations.

The apes of the subfamilies Homininae and Kenyapithecinae that dispersed from Africa underwent a considerable radiation in Eurasia until the end of the Mid-Miocene, around 7–9 Ma (Andrews and Bernor 1999). In Africa, apes are scarce between perhaps 15 Ma and the very end of the Miocene (Andrews and Humphrey 1999; Leakey and Harris 2003), although fragmentary specimens are known from some 10 Ma onward (Begun 2009*)*. Interpreting such scarcity in the fossil record is always hazardous, since it may indicate no more than an absence of suitable deposits or inadequate search and recovery. But if it is a real pattern, then it is perhaps the ancestor for the later great ape and human lineage of the subfamily Homininae may be found among these Eurasian advanced hominid apes. The possibility that the European Dryopithecini make the most plausible candidates has been both proposed (Begun 1993, 2009) and questioned (Andrews 1992; Andrews and Bernor 1999) on several details of taxonomy and systematics, but Solounias et al. (1999) raised the question again in the context of understanding wider issues of the relationship between faunas of southeastern Europe and Africa. The latter authors point out that many of the savanna-dwelling mammals of Africa may well have originated in what they term the Pikermi Biome, based on the rich Late Miocene Greek locality of Pikermi. They cite somewhat longer necked and thus more advanced giraffes, rhinos of the extant genera *Diceros* and *Ceratotherium*, the false sabretoothed cat *Dinofelis* and the larger bone-smashing hyenas *Belbus beaumonti* and *Adcrocuta eximia* as offering primary evidence for such an origin, and it is indeed clear that such animals do make their first appearance in Africa in the latter part of the Miocene. Overall, by around 8 Ma, over the middle part of the Miocene, there is an evidence of considerable incursion from Eurasia generally into Africa if we add to the above list the smaller to midsized and dog-like hyenas of the genera *Protictitherium*, *Ictitherium*, *Hyaenictitherium*, *Lycyaena*, and *Hyaenictis*, the sabretoothed cat *Machairodus*, a range of mustelids, and a number of antelopes (Vrba 1995; Werdelin and Turner 1996; Turner and Antón 2004). The impetus for this movement appears to have been a major shift in climate, changing the western European vegetation from subtropical evergreen forest to more deciduous and dry woodland and provoking a turnover in mammalian fauna that Agustí et al. (1999) termed the mid-Vallesian Crisis. By around 9 Ma, the dryopithecine hominids were extinct in Western Europe, although they managed to survive until perhaps 7.5 Ma in Italy and China (Andrews and Bernor 1999). A movement of early hominid apes back into Africa is therefore entirely plausible as part of this larger pattern of dispersion.

Zoogeography of African Pliocene Hominini

Whether or not the common ancestor of later Hominidae was indeed of Eurasian dryopithecine-like morphology and origin, our African ancestors and relatives changed from being generalized apes to more sophisticated apes with tools over a period of a few million years, only becoming really recognizably human with the earliest appearance of the *H. erectus* lineage at around 1.8 Ma. This transition included shifts to an upright stance and fully bipedal walking and a massive increase in relative and absolute brain size, presumably accompanied by alterations in behavior, social interactions, and intelligence. Details of zoogeography however remain unclear.

The earliest currently known putative hominins are from the late Miocene – *Sahelanthropus tchadensis* (6–7 Ma) from Toros Menalla in the Chad Basin (Brunet et al. 2002), *Orrorin tugenensis* (6.2–5.5 Ma) from Lukeino in Kenya (Senut et al. 2001), and *Ardipithecus kadabba* (5.77–5.2 Ma) from Gona in Ethiopia (Haile-Selassie and WoldeGabriel 2009). Both *O. tugenensis* and *Ar. kadabba* have been associated with wooded environments with a nearby water source, but the Chad Basin paleoenvironment appears to have been more of a mosaic association of lake-side gallery forest, wooded savanna, and open grasslands (Vignaud et al. 2002), and the precise preference of the primate is hard to determine (see Strait et al., chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3 and Rowan and Reed, chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1).

According to interpretations of the Early Pliocene material referred to *Ardipithecus ramidus*, first found in 4.4 Ma deposits of the Middle Awash Valley in Ethiopia (White et al. 1994, 1995), an attachment to a woodland habitat may have persisted until close to 4.0 Ma (WoldeGabriel et al. 1994). Material also referred to *Ar. ramidus* from 4.5 to 4.3 Ma sediments to the west of the Awash at As Duma (Semaw et al. 2005) is also said to be associated with moderate rainfall grassland and woodland/grassland, based on paleosols, soil carbonates, and faunal elements. However, stable carbon isotope values for ungulate dental enamels at the Gona *Ardipithecus* sites suggest a significant component of C_4 grasses in the diet (Levin et al. 2008), and we should beware of the dangers of a small number of early hominin localities misleading us about habitat preferences and true distributions.

We do know that the physical and biotic environment within which the hominins were evolving was itself undergoing significant changes. Rifting, volcanic activity, and uplift were continuing to change the topography of eastern and southern Africa as they had throughout the Miocene (Pritchard 1979; Adams et al. 1996), and as a result of these changes and their interaction with climatic events, the vegetation was opening out to provide the distribution and huge mosaic of habitats existing there today. Such physical and biotic changes underlie the distributions of the living African mammal fauna (Grubb 1999; Grubb et al. 1999) and must have had a major bearing on the zoogeography of the past (Turner 1995). Clearly, more open vegetation not only developed during the Pliocene but also became an attractive habitat for predators and in all probability early hominins (Turner and Antón 1999). The development of stone-tool technology can now be traced back in Africa to around 2.6 Ma at Gona in Ethiopia, and similarly dated stone-tool cut-marked bones have also been reported from Bouri in Ethiopia (Semaw et al. 2003). More recently, bones with damage interpreted as hominin-inflicted and dating from approximately 3.9 Ma have been reported from Dikika, Ethiopia (McPherron et al. 2010);

however, these have not been widely accepted (see Dominguez-Rodrigo et al. 2011 and references therein). What happened in terms of hominin development before such lithic technology was developed, either to assist or to motivate the move to more open terrain, is unclear.

An analysis of the zoogeography of African Pliocene hominins within the larger context of distributions in the rest of the Plio-Pleistocene large-mammal fauna was undertaken by Turner and Wood (1993), prior to the more recent discoveries referred to above but based on a larger body of hominin species and known distributions. The evidence available then, as now, suggested that the genus *Australopithecus* was apparently geographically split, and represented by *A. afarensis* in eastern Africa and *A. africanus* in the south. The genus *Paranthropus*, taken by Turner and Wood (1993) to be monophyletic, was considered to be represented by *P. robustus* and perhaps *P. crassidens* in the south and by *P. aethiopicus* and *P. boisei* in the east. More recent discoveries have extended the range of named hominin taxa in the eastern region but done little to alter that picture of regional distributions, although Bromage and Schrenk (1995) have extended the range of *P. boisei* southward to Malawi. The most primitive australopithecine species, *A. anamensis*, dating to approximately 3.9–4.2 Ma has been identified in both Kenya (Leakey et al. 1995) and Ethiopia (White et al. 2006), while another, *A. bahrelghazali*, has been recognized at Koro Toro in Chad in deposits of slightly later age (Brunet et al. 1996). A third species, *A. garhi*, has been identified in deposits of the Middle Awash Valley (Asfaw et al. 1999), and a fourth, placed in a new genus as *Kenyanthropus platyops* (Leakey et al. 2001), has been identified from deposits dated to 3.5 Ma at West Turkana. The newest (and latest) species of *Australopithecus* – *A. sediba* – has recently been recognized and dated to 1.97 Ma at Malapa in South Africa (Pickering et al. 2011).

In the case of the genus *Homo*, assessing the geographic distribution of species is made more difficult by the increasingly evident fact that the taxonomy is more complicated than has previously been assumed. *Homo* is conventionally considered to be evident in Africa back to about 2.5 Ma, first represented in eastern Africa by the species *H. habilis* and *H. rudolfensis*, although the latter has also been identified in Malawi by Bromage and Schrenk (1995). The fact that stone tools appear in the archaeological record at about the same time has led to speculations about the relationship between evolutionary change and the development of tool-making abilities. However, it has long been apparent that the earliest taxa assigned to the genus *Homo* are a rather heterogeneous group (Wood 1991, 1992), and it has been argued that they could be removed from *Homo* altogether, in a scheme leaving *H. erectus sensu lato* as the earliest clear member of the genus (Wood and Collard 1999; see also Wood and Baker (2011), Schrenk et al., chapter "▶ The Earliest Putative *Homo* Fossils," Vol. 3, Baab, chapter "▶ Defining *Homo erectus*," Vol. 3, and Tattersall, chapter "▶ *Homo ergaster* and Its Contemporaries," Vol. 3). This would place the first evidence of our genus within the Olduvai Event (1.95–1.77 Ma) and sometime after the earliest appearance of stone tools, and it is this seemingly abrupt appearance of *H. erectus* that has led to suggestions of a possible origin outside Africa (White 1995; Dennell 2004).

Of course, tool making by hominins of other genera is neither improbable nor implausible. Chimpanzees both make and use tools, albeit primitive ones that satisfy any sensible definition of such behavior, and it may be that a variety of evolutionary solutions that included some elements of manufacture and use of technology were developing among the African Pliocene hominins (Turner and Antón 2004). While our own lineage moved toward greater ecological generalization coupled to an emphasis on stone-tool technology and an increase in brain size, members of the genus *Paranthropus* appear to have developed larger jaws and teeth in order to cope with their food (see Rowan and Reed, chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1). At least one hominin species traditionally referred to *Homo*, the east African *H. rudolfensis*, appears to have followed the same path as the paranthropines between 2.5 and 1.8 Ma with enlarged teeth but with a relatively large brain as well. If the *H. rudolfensis* material is indeed to be linked to the earlier *K. platyops* and referred to that genus, as suggested by Leakey et al. (2001), we may then very well have evidence of a separate lineage within which brains and teeth both developed. We may therefore identify at least three different evolutionary developments within Pliocene hominins, all of which enjoyed a considerable measure of success.

Whatever the lineages involved, making sense of the zoogeography of Pliocene hominins is difficult. The record presents a complex series of morphologies and proposed taxa, and interpretations of identity, relationship, and adaptations of the various species, leave alone distributions, are impeded by the fragmentary state of much of the material and the fact that several taxa or putative taxa are represented by single specimens or localities. This underscores the value of looking at distributions within the rest of the fauna in order to see whether patterns that may appear to be present in the hominins make sense in terms of larger-scale patterning. The investigation by Turner and Wood (1993) extended to include just such a larger patterning in eastern versus southern African taxa and concluded that there was evidence for a high degree of regional differentiation in some families, particularly the Bovidae, coupled with evidence for significant dispersals in others. Among the Primates, the papionin monkeys appeared to show the most evidence for dispersals, and overall, it was apparent that regional isolation was not a matter of rigid demarcation. The implications of this for our understanding of hominin biogeography are that regionally restricted taxa would be a plausible interpretation of the material to hand, but that movements between regions are likely to have occurred and that identified genera such as *Australopithecus* and *Paranthropus* with differing species in each regions are indeed likely to be monophyletic. If monophyly is a correct interpretation, then a localized origin with subsequent dispersals is likely to have been the dominant pattern (Turner and Paterson 1991; Turner 1999a).

The known distribution of Pliocene and perhaps Late Miocene hominin remains now stretches from Chad down through eastern Africa to South Africa, perhaps even from the Atlantic coast of the western Sahel down to the Cape as Brunet et al. (1995) argued, and any reasonable interpretation of that pattern would recognize it as a minimal statement of range. But how much the gaps in between known localities were filled in, or the limits of distribution extended, remains unknown. Artifactual evidence from northwestern Africa may indicate the presence of hominins with Oldowan tools as early as the Olduvai event (Sahnouni and van der Made 2009), but the best evidence appears to date from around 1.0 Ma (Raynal et al. 2001). Dennell (2004) has even suggested that if Pliocene hominins were in Chad some 2,500 km west of the Rift Valley by 3.5 Ma then why not as far to the north or east by the same period? This, of course, would place them in southwestern Asia.

Out of Africa

The number, timing, and direction of earliest hominin dispersals from Africa have long been a major point of discussion, and opinions on these topics remain varied and contentious (Rolland 1998; Turner 1999b; Bar-Yosef and Belfer-Cohen 2001; Strauss 2001; Villa 2001; Dennell 2004, 2009; Abbate and Sagri 2012). Early Pleistocene assemblages from ‘Ubeidiya in Israel dated to around 1.5 Ma (Belmaker et al. 2002), perhaps Pakistan by 1.8 Ma (Dennell 2004), Iberia by 1.4 Ma (Oms et al. 2000; Toro-Moyano et al. 2013) and human material from Dmanisi in Georgia dated around 1.8 Ma (Lordkipanidze et al. 2013) set a minimal date for the original movement. Dispersals to eastern parts of Asia remain more contentious (see Dennell (2009) for review), with the best evidence so far from 1.66 Ma deposits with stone implements and what is interpreted as stone-tool processing of animal carcasses at Majuangou in the Nihewan Basin of northern China (Zhu et al. 2004). The stone tools resemble primitive Oldowan items found in African deposits, and the authors argue for a significant and flourishing early dispersion from Africa, although the rest of the mammalian fauna has no clear African elements. Hominin occupation appears to have been more extensive and intensive in Europe in particular and Eurasia in general after 0.5 Ma with a long tail of more sporadic appearances back into the Early Pleistocene (Turner 1999b; Roebroeks 2001), although Martínez et al. (2010) suggested that occupation in Iberia *may* have been continuous from the latest Early Pleistocene. But which route, or routes, was used? Several have been proposed – land across Sinai and the Levant, across the Bab el-Mandeb Straits at the south of the Red Sea and then across the Arabian Peninsula proper, or by the Gibraltar Straits? Here the evidence is reviewed from a faunal perspective, but see Abbate and Sagri (2012) for further information on the geomorphology.

Gibraltar

Although the evidence available points to some part of the Arabian Peninsula as the most probable route for Plio-Pleistocene hominin dispersions, a route across the Gibraltar Straits has frequently been proposed. For example, Rolland (1998) argued for a reduction of the seaway through the Straits to 8 km during glacial maxima, without any increase in surface current and for sweepstake-like movements, especially during OI Stages 12 and 16. Flemming et al. (2003) argued that the Strait itself would not have narrowed significantly during sea-level falls, although they pointed out that now submerged areas to the west of the Strait would have formed substantial islands that might have provided "stepping stones." Strauss (2001, p. 99) offered a thoughtful analysis of the issue but concludes that the record for human contacts is "at best spotty and ambiguous." As far as other routes across the Mediterranean are concerned, particularly between Tunisia and Sicily, Flemming et al. (2003) reached no conclusion, and it is not evident that such possible routes have any strong scientific support. Villa (2001) provides a useful summary of some of the arguments and rejects the idea of such routes.

As summarized elsewhere (O'Regan et al. 2006), among the extant and Holocene terrestrial mammals present in North Africa and Iberia, such as wild boar (*Sus scrofa*), red deer (*Cervus elephas*), otter (*Lutra lutra*), and the red fox (*Vulpes vulpes*), there are none that are not also present in the Levant. This suggests that these animals took a circum-Mediterranean route rather than crossing the Gibraltar Straits (Dobson 1998), although of course, the possibility of some individual animals swimming across cannot be completely ruled out. Some bat species are found on both sides of the Straits and further eastward in Europe but are not recorded in the Levant or elsewhere in North Africa, which could imply dispersion across the Gibraltar Straits (Dobson and Wright 2000). However, the extent to which recent human interference has played a part remains a concern, and of the 17 terrestrial mammal species inhabiting North Africa today only four are considered to have a natural circum-Mediterranean distribution, whereas the rest are thought to be recent introductions (Dobson 1998). Clearly, if populations of *H. sapiens* were capable of dispersing over substantial bodies of water to reach Australia in the Late Pleistocene (Bowler et al. 2003), then it is also possible that they may have been moving around the Mediterranean and transporting animals prior to the Holocene, a point stressed by Strauss (2001). However, the Gibraltar Straits cannot be shown convincingly to have been the scene of natural Pliocene, Pleistocene, or even Holocene movements of terrestrial mammals (with the possible exception of the hippopotamus (O'Regan 2008)) and thus the Arabian Peninsula remains the only established route of a two-way movement between continents.

Arabia

In contrast, the possibility of hominin dispersions through the Arabian Peninsula and the Levant, either across the Sinai Peninsula or the Bab el-Mandeb Straits at the south of the Red Sea, is indicated by the mixed Afro-Eurasian nature of the fauna of the region since the later part of the Pliocene and in particular by the Early Pleistocene deposits at 'Ubeidiya in Israel (Tchernov 1992; Belmaker et al. 2002; Belmaker 2010a). Later Pliocene African elements, chiefly bovids and giraffids, are known to the north of the Taurus-Zagros mountain chain that borders the northern boundaries of the Arabian Peninsula at localities such as Kuabebi in the Caucasus and Wolacks in Greece (Sickenberg 1967), the Oltet Valley in Romania

(Radulesco and Samson 1990), and Huélago in southern Spain (Alberdi et al. 2001). However, many of these taxa have now been reinterpreted as Miocene relicts rather than African immigrants, leaving relatively little evidence for Late Pliocene and Early Pleistocene African dispersals (Agustí et al. 2009; Agustí and Lordkipanidze 2011). Reviews of faunal dispersal both into and out of Africa between 3.0 and 0.5 Ma can be found in O'Regan et al. (2011) and Martinez-Navarro (2010).

The evidence for African faunal elements at Dmanisi has recently been reviewed and largely discounted by Agustí and Lordkipanidze (2011); while at 'Ubeidiya the African faunal affinities were based on an undetermined giraffid, the bovids *Pelorovis oldowayensis* and *Oryx* sp., the hippo *Hippopotamus gorgops*, the suid *Kolpochoerus olduvaiensis*, and a number of carnivores including the spotted hyaena, *Crocuta crocuta* and possibly the honey badger cf. *Mellivora* sp. (Tchernov 1992; Belmaker 2010). The Acheulean industry at 'Ubeidiya is unknown at Dmanisi and appears to have developed in Africa at a slightly later date. Other Early Pleistocene localities in Europe have relatively few African species. Much has been made of the appearance of the cercopithecine *Theropithecus* cf. *T. oswaldi* at Cueva Victoria in southeastern Spain (Gibert et al. 1995), and possibly at Pirro Nord in Italy (Rook et al. 2004) and 'Ubeidiya (Belmaker 2010b), and of the African machairodont cat, *Megantereon whitei*, at Venta Micena, Dmanisi and the Greek locality of Apollonia (Martínez-Navarro and Palmqvist 1995, 1996; Palmqvist et al. 2007). The *Hippopotamus*, is also present at several Early Pleistocene sites such as 'Ubeidiya and Venta Micena (O'Regan et al. 2006, 2011).

Overall, the suggestions of possible hominin dispersions into Eurasia during the very earliest Pleistocene that appear in the literature from time to time (Bonifay and Vandermeersch 1991; Boitel et al. 1996), while unsupported by critical assessments of the evidence within Eurasia, cannot be dismissed a priori as impossible or even unlikely. These conclusions parallel some of those reached by Mithen and Reed (2002) in their computer simulation of dispersals and stressed elsewhere (Dennell 1998, 2004). If recent arguments summarized earlier about the status of later Pliocene species referred to the genus *Homo* are correct, then clearly the earliest hominin to have moved out of Africa would not have been a member of our own genus. However, whether such a view offers support for an extra-African origin for *H. erectus* remains unclear, particularly as the latest data from Dmanisi appear to demonstrate that the cranio-dental morphological variability seen in *Homo erectus*, *H. ergaster*, and *H. georgicus* are all present within the specimens from this single locality (Lordkipanidze et al. 2013; see also Baab, chapter "▶ Defining *Homo erectus*," Vol. 3 and Tattersall, chapter "▶ *Homo ergaster* and Its Contemporaries," Vol. 3).

Precise Routes

If Arabia is indeed the only plausible route out of Africa for terrestrial mammals during the Plio-Pleistocene, it remains difficult to judge the relative contributions of the Sinai versus the Bab el-Mandeb as gateways. While knowledge of the Middle Paleolithic or later Middle Pleistocene hominin occupation of Arabia is rapidly improving (e.g., Crassard et al. 2013), there is still a relative paucity of evidence for Lower Paleolithic occupation (Petraglia and Alsharekh 2004). However, as Petraglia (2003) also showed, both Oldowan and Acheulean assemblages are known, and the eastern side of the Bab el-Mandeb Straits in particular appears to have been occupied by hominins with this technology. Unfortunately, the absence of good chronological control remains a major obstacle to assess the pattern of lithic assemblage distribution.

As Petraglia and Alsharekh (2004) show, while movement across Sinai offers the possibility of movement along the Levant and then perhaps south into Northern Arabia either along the eastern Red Sea Coast or inland behind the highlands of the Hejaz Asir, movement across Bab el-Mandeb confronts any dispersing population directly with the highlands. These would tend to restrict movement to the coastal strips, north along the eastern Red Sea Coast or east along the Arabian Sea Coast. While annual rainfall today in the Hejaz Asir or in the Oman Mountains at the easternmost corner of the Peninsula can reach well over 100 mm, much of the southeastern portion, the Rub Al Khalil or Empty Quarter, may have no more than 50 mm with temperatures that exceed 50 °C (Glennie and Singhvi 2002). The fact that Lower and Middle Paleolithic occupation did occur means of course that conditions were sometimes favorable, and substantial river systems appear to have existed certainly by MIS 5 (Crassard et al. 2013), but lack of evidence hampers interpretation of the earliest hominin dispersals. Little is known of the Plio-Pleistocene fauna of Arabia, which is even more sparsely represented than that of the Miocene. The sole exceptions are the small assemblages from An Nafud in northern Saudi Arabia, thought to be of Early Pleistocene age (Thomas et al. 1998) and which, with spotted hyaena, hexaprotodont hippo, horse, elephant (cf. *Elephas recki*), several bovids including a species of *Pelorovis* as well as crocodile and fish, are of distinctly African stamp. The range of species implies good grassland and standing water in the vicinity, an interpretation supported by isotopic analyses of herbivore teeth.

However, as Glennie and Singhvi (2002) also point out, increased aridity is indicated during glacial periods, beyond even that seen today despite the fact that temperatures may have averaged somewhat lower, and this factor presumably played a large part in determining the extent to which mammals, including early hominins, could maintain any occupation throughout the Pleistocene. Current data indicate that these periods of aridity are related to the deposition of Aeolian sands over at least the last 0.2 Ma (Preusser 2009). Glacial periods with related sea-level changes are of course precisely the point at which the Bab el-Mandeb crossing is likely to have been at its most obvious and navigable to early hominins (Rohling et al. 1998; Cachel and Harris 1998), so that the easiest and most attractive access by that route is likely to have been at a point when conditions in southern Arabia, and for that matter on the corresponding coastal area of Africa, are likely to have been least appealing. Taken overall, the Bab el-Mandeb Straits do not seem likely to have offered a likely gateway out of Africa for terrestrial mammals during the Lower and Middle Pleistocene, suggesting that movement across Sinai and then northward along the Levant, southward into Arabia, or eastward and beyond is the most plausible route. However, movement across the Bab el-Mandeb during the later Pliocene, before the Straits had fully formed, and thus before the crossing into Arabia was dependent on sea-level fall, may have been an entirely different matter, as previously pointed out (Turner 1999b). The importance of the Afar region of Africa to the south and west of Bab el-Mandeb as an area of attractive resources for mammals, including hominins, following rivers into the developing depression as rifting progressed from Miocene times onward was highlighted by Kalb (1995, p. 366), who stressed "the step-by-step process of animal migrations into and dispersal across inter-continental areas prior to complete plate separation."

Conclusions

It seems clear that the wider context of movements between Africa and Eurasia throws useful light on the patterns of dispersion within Primates in general and Hominoidea in particular so that changes in primate distribution can be examined without having to treat them as a special case. In the earliest stages of the Oligocene and Early Miocene, we see that movements into Africa are accompanied by a range of other taxa. If dryopithecine apes first moved back into Europe during the Mid-Miocene and then back again into Africa toward the end of that epoch, then they did so as part of a much wider dispersal across a range of mammalian orders.

Current knowledge of Pliocene hominins is at best incomplete, and while recent discoveries have extended the range of named species, they have done little to clarify the likely relationships between those taxa or the true nature of distributions. With the greater number of putative taxa now available, it will require some considerable time and quite a few more discoveries before real sense can be made of the patterns. However, as far as movement out of Africa by hominins is concerned, a number of points can be made. The Gibraltar Straits are unlikely to have been the site of any Pliocene or Pleistocene gateway for terrestrial mammals, and while movement across the Bab el-Mandeb region before the Red Sea opened fully toward the end of the Pliocene may have been possible, dispersal across the Straits once the glacial and interglacial cycle got underway seems to us unlikely. Sinai and the Levant, the scene of a two-way faunal movement between continents during the latest Pliocene and earliest Pleistocene, remains the only established route. Moreover, the diversity of elements using that gateway points to the relatively hospitable nature of the area in the Earliest Pleistocene, so that suggestions of possible hominin dispersions into Eurasia during this period are not inherently implausible. However, how long any dispersing populations were able to maintain their extended range is entirely another question. Early hominin movements into Arabia and the Levant may have been sporadic, and probably tenuous and subsequent movements out into Eurasia proper were probably even more so.

Cross-References

- ▶ Defining *Homo erectus*
- ▶ Defining the Genus *Homo*
- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Fossil Record of Miocene Hominoids
- ▶ The Biotic Environments of the Late Miocene Hominoids
- ▶ The Earliest Putative *Homo* Fossils
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ The Species and Diversity of Australopiths

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The Paleodemography of Extinct Hominin Populations

Janet Monge and Alan Mann

Contents

Abstract

Paleodemography is the study of past population structure. The demographic structure of the population is both the outcome of evolutionary processes operating on groups of individuals and the basis on which future evolutionary forces can potentially operate. This review is concerned with a critical evaluation of paleodemographic studies of the hominin lineage prior to the development of agriculture. Because of the potential this research has for the generation of data about birth spacing, mortality, lifespan, sex ratio, patterns of fertility, and maturation, the study of the demography of earlier human populations has attracted much attention. Very limited and fragmentary sample sizes, however, combined with many uncertainties about depositional patterns, have led to major

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J. Monge (✉)
Department of Anthropology, University of Pennsylvania, Philadelphia, PA, USA
e-mail: jmonge@sas.upenn.edu

A. Mann
Department of Anthropology, Princeton University, Princeton, NJ, USA
e-mail: mann@princeton.edu

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difficulties in the development of generally accepted hypotheses. Because of the nature of the preservation of skeletal materials, oftentimes past population structure has been modeled on known living populations. In the remote past, for example, at the inception of the human lineage, the choice of comparative living samples from which to derive models is problematic. Are the data from chimpanzees or modern humans more appropriate in these reconstructions? Or are the past and extinct populations completely different from any other population model constructed from living species?

Since many population parameters are based on life history variables, and vice versa, the assessment of population parameters in the past must be based on an effective evaluation of those key features that influence virtually every aspect of population structure: mortality, fertility, and longevity, to name just a few. Published reevaluations of a number of widely accepted concepts, such as the simple association of life history variables with structures like gross body or brain size, have made these earlier studies increasingly untenable. Further, recently collected data on modern humans and free ranging chimpanzees has cast doubt on the idea that these two primates experience dramatically different timing in their maturation and lifespan events. Other life history parameters of extinct populations, however, such as life expectancy, age at maturation and age at weaning may be retrievable.

While there are many useful variables of past population structure that can be analyzed, most social/cultural parameters (see Layton et al. 2012) cannot be retrieved from the earliest phases of human evolutionary history. These include settlement size and household size and especially changes in population size over time, growth, decline, and even population collapse.

Introduction

Demography is the study of population structure, its size, composition, and related features such as sex, age, geographic distribution, and other environmental, social, and cultural factors. The successful application of demographic studies in modern human societies relies on the accumulation of data on all members of a population or, more commonly, on a calculated sampling of the population (Yaukey and Anderton 2001). In contrast, paleodemography has been characterized as the field of inquiry that attempts to identify demographic parameters from past populations derived from archaeological contexts (Hoppa 2002, p. 9) (Bocquet-Appel 2010) and is primarily based on the analysis of human skeletal materials. The preservation of human skeletons in contexts of even the relatively recent prehistoric past, where agriculture and permanent settlement are present, is variable and dependent on environmental conditions such as soil type and pH, climate, and destructive geological events. Additionally, cultural factors, such as cremation, cannibalism, mass burials, indifference to the disposition of dead infants, and many other behavioral factors, also dramatically influence the preservation of human bones. This chapter is limited to an examination of the paleodemography of our earlier ancestors, prior to the development of agriculture.

Reconstructing population structure from this more distant past is much more problematic. Some recent notable technical advances include the modeling of life tables for preindustrial human populations, predicting mortality patterns (Seguy et al. 2010) and, in the analysis of the skeletal series at Libben, exploring the fertility patterns in a nonagricultural village (Meindl et al. 2010).

Population size, although strictly not a demographic parameter without other information about the structure of the population, has been used to understand factors like extinction in previous hominin populations using archaeological site samples from Western Europe (Mellars and French 2011; critiqued by Dogandzic and McPherron 2013) and to explain the genetic structure of modern human populations (Hawks 2010).

Preagricultural hominins, it has been postulated, relied on a subsistence base founded on the gathering and collecting of wild foods, insects and small vertebrates, and the hunting of larger animals. Scattered and seasonally available food sources meant that for the most part, these peoples did not have permanent settlements. Rather, they established temporary camps, exploiting the local resources and moving on when these were depleted. The duration of a stay at a particular locale was dependent on the season, abundance of resources, size of the group, and other variables. The groups were small in size (Weiss 1973) often no larger than 30–50 individuals. Based on modern ethnographic examples (i.e., Lee and Devore 1968), groups were probably seasonally variable in membership. Temporary encampments and continuous movements imply that deaths would have occurred at different places and that, except for unusual circumstances, we should not expect to find remains of a number of individuals at a specific locale. The expectation is that many deaths will occur during movements and the body left or interred, along the route. Further, deaths would have been seasonal, occurring during those times of the year when resources were scarcest; this implies that hominin remains are more likely to be found at some locales and not others. These generalizations about early members of the human lineage, however, are overwhelmingly based on the anthropological study of living gatherers and hunters, and the accuracy of these observations when applied to earlier, now extinct humans, is uncertain (chapter "▶ Modeling the Past: The Primatological Approach," Vol. 1). Layton et al. (2012) make the argument that the basic life and demographic parameters of a gatherer/hunter society were achieved by the time frame of *Homo heidelbergensis* (viewed by some as archaic *Homo sapien*s). There is, for example, no certainty that all earlier hominins actually were gatherer/hunters; they may have been more specialized in dietary choice and habitat and thus were organized in a different but unknown fashion. As there are periods in the hominin fossil record which suggest that multiple hominin species coexisted, perhaps in geographically close proximity, it remains possible that early hominin demography was based on very different adaptive patterns. Further, prior to about 115 Ka, the sample of hominin skeleton bones available for study is very small. Only after this time did the introduction of the deliberate burial of the dead result in many more bodies being preserved, and numbers of more or less complete skeletons excavated. Finally, the study of the earliest known members of the hominin lineage, mainly early members of the genus *Homo* and still earlier species of the genus *Australopithecus*, is fraught with difficulty (for the moment, fossil samples of the very earliest identified hominins, *Sahelanthropus* and *Orrorin*, are much too few even to be considered here). The *Ardipithecus ramidus* sample, while quite extensive (see collected papers in *Science 326*, 2009), remains relatively unknown from the perspective of demography. Bones of these creatures are discovered in very different circumstances than later hominins. These early remains are usually broken and very fragmentary; multiple bones from the same individual are rarely discovered. The deposits in which they have been preserved have been formed by long-term geological processes; and they are not directly associated with archaeological accumulations. The reconstruction of the taphonomic circumstances that led to the hominin bones being deposited in the geological sediments in which they were found is complex and often ends with uncertain results. However, survivorship curves have been developed recently on the dinosaur species *Albertosaurus sarcophagus* by Steinsaltz and Orzack (2011), an approach that might hold some promise in the analysis of fossil hominins in deep evolutionary time.

The study of general paleodemographic variables is therefore limited by the recovered skeletal and fossil samples and their contexts. These do not yield valid population samples for the construction of the sort of demographic profiles possible in the study of extant humans. Thus, the techniques of analysis and the modeling of data accumulated on these skeletal samples, even under the best of circumstances, can provide only the most preliminary and shadowy details about population structure and basic life history variables.

Basic Parameters of Paleodemographic Study

Estimation of the Age at Death of Skeletal Remains

A demographic study of a skeletal sample begins with the assessment of both the age-at-death and sex distribution of the skeletal material. These data are absolutely essential for the construction of other population statistics. Aging and sexing of skeletal samples of living humans has been the subject of extensive research focused on the development of techniques that can yield results with a high degree of accuracy. The problems associated with aging and sexing and the ways in which the resultant data have been modeled have been summarized by Hoppa and Vaupel (2002). When the sample is of nonmodern skeletal materials (e.g., Neanderthals or australopithecines), the criteria for judging these factors are far from certain. Establishing the age at death of a skeleton relies on knowledge of the life history of the species concerned and of the biological pathways within which these hominins grew and matured. There remains uncertainty and debate about the timing of maturational events in the dentition or the skeleton and about whether models based on living humans or chimpanzees provide greater accuracy. Recent considerations of the variation in growth that characterizes chimpanzees and living humans add a further complication to these estimations (Zihlman et al. 2004;

Smith and Boesch 2010; Monge and Mann 2006). In their summation of the *Ardipithecus ramidus* materials, White et al. (2009) argue that the anatomical features of these primates indicate that "the last common ancestors of humans and the African apes were not chimpanzee-like and that both hominids [hominins in this review] and extant African apes are each highly specialized, but through very different evolutionary pathways" (White et al. 2009, p. 64). If this conclusion is confirmed by additional research, the use of chimpanzee biology in reconstructing early hominin lifeway patterns will need to be seriously reconsidered.

Although they are often considered together as part of a single aspect of paleodemography, it is our contention that potential life variables, including lifespan (often referred to as the study of life history), should be dealt with separately from a consideration of the achievement of this life potential (which is often viewed as a central focus of paleodemographic studies). Potential lifespan is an evolutionary biological phenomenon (with important implications for the evolution of culture) whereas achievement of that life potential represents the complex interaction of biology and culture. Carey and Judge (2001) aptly summarized this dichotomy when they observed that modern humans probably achieve a level of life potential far earlier than this potential can be routinely achieved. Through biomedicine, diet, sanitation, insect control, and other cultural appliances, modern societies have been attempting to reconcile these two elements: to make life potential and individual lifespan the same phenomenon, not just for a favored few but for all humans. In reality, while all living human populations have the potential for the same potential life expectancy (Carey and Judge 2001), most people do not achieve this. Comparisons of differences between populations are one way to analyze the contributions and adequacy of cultural mechanisms to achieve this potential and are of possible use in paleodemography. For example, using a sample of 768 dental individuals spanning the course of most of human evolution, Caspari and Lee (2004) have argued that increased cultural complexity was primarily responsible for the increases in lifespan during the course of the latter phases of human evolution.

When and under what circumstances members of the human lineage achieved a modern humanlike potential life expectancy is a matter of some debate. This includes debates on all phases of life history, from infancy through childhood and adolescence to adulthood. More fundamentally, even statements that the potential of life expectancy in humans is double of that in chimpanzees must now be questioned, especially the statement that potential lifespan in humans is double that of chimpanzees. Maximum age for humans is frequently quoted as 90–100 years, and 50 years for chimps (Sacher 1975; Hawkes et al. 1998; Bogin 1999). However, our knowledge of the lifespans of chimpanzees is presently limited to a few known-age captive animals and is hampered by the paucity of field observations of wild chimpanzees, even though some have been observed for 40–50 years. Cheeta, the chimpanzee who was featured (in all likelihood) in the Tarzan movies, died in 2011 at the age of 80 (or so it was claimed).

The chimpanzees of Mahale have been studied for 34 years and are now providing a limited demographic data set that suggests death among older animals occurs between 31 and 48 years (Nishida et al. 2003). This is not radically different from the profiles of average age at death in many pre-1900 human populations and for what has been estimated for most of human history (Gage 2000; but see also Ascádi and Nemeskéri 1970, and see Robb 2007 for a discussion of the age at death in preindustrial France). The Mahale chimpanzee study also reports that approximately 25 % of older females had a postreproductive lifespan. This phenomenon, the equivalent of postmenopausal human females, has traditionally been cited as a uniquely human life history event. From these observational data, it is clear that this postreproductive phenomenon can no longer be considered a unique event in human life history; theories that have been associated with this pattern, e.g., the grandmother hypothesis, must be reconsidered in light of this data (Alvarez 2000; Hawkes 2003; Levitis et al. 2013), although it is possible that the extent of these postreproductive years might be greater in humans (Blurton Jones et al. 2002).

Since the process of aging causes an exponential increase in virtually all pathologies (Harrison and Roderick 1997), evolutionary selection for increased longevity must target the genes responsible for aging and not focus exclusively on a reduction in fatalities associated with pathological conditions. In baboons, longevity has a reasonably strong genetic component (Martin et al. 2002), and it is possible that chimpanzees and humans have the same potential for longevity; via cultural mechanisms, humans have reduced the cumulative effect of pathological conditions directly associated with aging. Vaupel et al. (1998) have provided a more detailed discussion of the effect of increases in longevity on human demography.

The causes of death in past populations are also difficult to determine. Nishida et al. (2003) have calculated that in the Mahale chimpanzees, just under half of deaths are caused by disease. This appears to exclude general causes associated with death by senescence. In a study of a population of chimpanzees in Guinea Bissau, Sugiyama (2004b) reported that under conditions of ecological stress, in this case deforestation, specific subsets of the group were more likely to die: infants (0–3 years of age), juveniles (4–7 years), and active adolescents (8–11 years).

Mortality profiles of five gatherer/hunter groups are presented in Hill et al. (2007). The primary cause of death reported for the Hadza, a gatherer/hunter group in Tanzania, between the years 1985 and 1997 (Blurton Jones et al. 2002), appears to be disease, here also excluding death associated with the state of just being old. Sugiyama (2004a) has reported on the extent of injury in a forager-horticultural group, the Shiwiar (Ecuador). The results of 678 injuries suffered by 40 individuals indicate that trauma is likely, in fact, common at all stages of life and that without group provisioning, the effects of these injuries would range from debilitating to lethal. If the same sorts of patterns existed in the past (Martin and Frayer 1997), it is reasonable to suggest that provisioning may have played a role in the social system of earlier hominin taxa. Berger and Trinkaus (1995) reported on the incidence and anatomical position of bone fractures in Neanderthals. The position and frequency indicated that the Neanderthals were living a challenging lifestyle with a preponderance of injuries on the upper part of the body. The Krapina Neanderthal collection also shows a significant number of nonlethal injuries

(Kricun et al. 1999), some of which appear to have demanded provisioning of some sort, for example, the Krapina 34.7 parietal in which a large cranial depression shows a considerable amount of posttrauma healing (Mann and Monge 2006). Indeed, death from trauma may have been the main cause of death in earlier hominins. It is, however, extremely difficult to identify signs of disease in earlier hominins because few diseases leave any sign of abnormal bone change (Roberts and Manchester 2007). Further, before the advent of plant and animal domestication, most of the pathologies that have killed millions of modern humans were not a part of the environmental stressors earlier hominins were exposed to. Diseases such as tuberculosis, influenza, rhinoviruses (common cold), bubonic plague, typhus, cholera, polio, typhoid, pertussis, and diphtheria are the result of human settlement after agriculture and the close associations that developed with domestic animals (Crawford 2007).

Except for the widespread signs of bacterial infection on the Middle Pleistocene Kabwe specimen from Zambia, virtually nothing is known about the cause of death in fossil hominins. Similarly, almost nothing is known about the cause of death in most recent human archaeological samples (see, e.g., a description of paleopathology in Lovell 2000). Pettitt (2000) argued, using the oldest aged Neanderthal skeletons, primarily Shanidar I and La Ferrassie 1, that life was difficult in the past and that death primarily resulted from repeated sustained trauma. He based this conclusion on the general robusticity of the Neanderthal skeleton, including dense bones and strong muscle markings which suggested that the body was repeatedly challenged in life. In contrast, X-ray analysis of the entire fossil skeletal sample from the site of Krapina (Kricun et al. 1999) concluded that the skeletons are of healthy individuals, with the dense bone structure indicative of an active lifestyle.

On the basis of assemblages of bones showing a lack of representation of very young and old individuals, Bocquet-Appel and Arsuaga (1999) have argued that at the two largest hominin fossil sites in Europe, Krapina, and Atapuerca (SH), the hominin accumulations were the result of a catastrophe. Cannibalism has been considered a possible cause for the accumulation at Krapina (White 2000); that at Atapuerca (SH) has been attributed to trapping of hominins by bears (but see also Bermudez de Castro and Nicolas 1997). The age distribution at these sites, with an overabundance of adolescents and young adults, fits the paleodemographic profile of skeletal materials caught in a catastrophic event (Paine 2000). The death profile of many catastrophes, for example, the tsunami in the Indian Ocean at the end of 2004, often illustrates the overwhelming overabundance of children including adolescents in the death assemblage; estimates calculate that at least one-third of the deaths in South East Asia were of children.

Carnivore activity is considered a possibly significant contributor to the australopithecine fossil assemblages in the South African dolomite caves (Brain 1981). In this instance, the preponderance of young (but not infant) individuals might be most reasonably explained by differential predation of the young, something that is documented for African ground-dwelling baboons (Mann 1975). Some sort of catastrophic event may apply to the proposed simultaneous death assemblage in the A.L. 333 site at Hadar, Ethiopia.

In a series of papers, Bocquet-Appel and colleagues beginning in 1982 (Bocquet-Appel 2010) have emphasized the difficulties of achieving dependable paleodemographic parameters from the aging of skeletons. He has argued that no matter how they are modeled, population profiles can only incompletely represent the living group from which they derived and only in one small slice in time. Further, considering the small, nonrandom sample sizes that are the usual subject of study, if the population from which the skeletons derive is in the process of demographic change, for example, in a general or even brief trend of population increase, then the resulting death assemblage is likely to show a preponderance of young individuals relative to the number of adults. The same pattern can also be explained by a general increase in population in-migration. Thus, without large sample sizes covering a longer time period, it would appear inappropriate to propose any broad generalizations.

Because of the nature of the fossil record, the bulk of efforts at aging concentrate on the dentition, the most likely element to preserve, although other parts of skeletal anatomy have also been used to age fossil skeletal elements.

In forensic anthropology, the determination of as precise an age at death as possible is crucial for individual identification. In paleodemography, this level of accuracy is not required and the use of life table modeling is considered to be effective. Nevertheless, derived age structure must be used to model the population appropriately in the first place, with the assumption that age-at-death differences in populations form an inherently interesting question. In human evolutionary studies, the age-at-death distribution question is an interesting one since it allows us to attempt to understand evolutionary process from the perspective of mortality.

One of the major critiques of paleodemography discussed by Bocquet-Appel and Masset (1996) involved the assumptions made in the process of aging a skeleton. This initiated a debate evaluating the criteria employed in the estimation of the age at death of skeletal samples (Bocquet-Appel 2010; Van Gerven and Aremelagos 1983; Greene et al. 1986; Konigsberg and Frankenberg 1994). Discussion focused on the use of aging standards based on the biases already present in the reference samples, to such an extent that the resulting aging profiles mimicked the age distribution of the reference sample. Bocquet-Appel and Masset's (1982) principal concerns about the limitations of paleodemographic studies include the assumptions that the populations from which the skeletons derived were stable, life history patterns were the same throughout human evolution, and mortality patterns in the past can be understood using recent human and primate populations. Many of these same points were made by Howell (1982) on a paleodemographic study of the Native American Libben Site, Ohio (Lovejoy et al. 1977). A review by Milner et al. (2000) evaluates the issues first raised by Bocquet-Appel and Masset (1982).

These discussions require critical appraisal of the published literature on the estimation of the age at death of the skeleton (for comprehensive reviews, see Katzenberg and Saunders 2000; White 2000; Hoppa and Vaupel 2002), and some skeletal biologists have advocated for the use of functional life history stages rather than age categories within the paleodemographic analysis of skeletal samples (Roksandic and Armstrong 2011). In many cases, these standards have been developed in the USA on the Hamann-Todd Osteological Collection (curated at the Cleveland Museum of Natural History, 1 Wade Oval Drive, Cleveland, Ohio 44106) and the Terry Collection (curated at the Department of Anthropology, Smithsonian Institution, Museum of Natural History, Washington DC 20013), both reference collections of known age- and sex-at-death individuals.

Early research that presented models of the lifespan of fossil hominins, summarized by Ascádi and Nemeskéri (1970), examined a variety of fossil hominin materials from Europe and Asia. Later, more elaborate discussions (Mann 1968, 1975; McKinley 1971) focused on the large fossil collection of *Australopithecus robustus* from the Swartkrans site in South Africa. On the basis of observed similarities in the pattern of dental development among the significant sample of immature individuals in the Swartkrans fossil collection to that established for modern humans, Mann argued that these early hominins matured in the prolonged period then thought to be unique to *Homo sapiens*. This conclusion was criticized by Sacher (1975, 1978), whose research on the correlation between brain size and longevity suggested that the life history trajectory of the small-brained robust australopithecines was more apelike than humanlike. Smith (1989) expanded on this work, arguing for a strong correlation between dental development and brain size. More recent data on primate biology has made some of Smith's conclusions untenable. For example, factoring in variations in diet, Godfrey et al. (2001) have shown that cranial capacity alone is an insufficient predictor of dental development within primate taxa. Although not frequently quoted in anthropological reviews of life history, Carey and Judge (2001), using a large longevity sample, have shown that brain size is only one of a number of central aspects of life history. Gage (1998) has also pointed out that in order to extrapolate to primate life history, more information is needed on patterns of variation, especially environmentally induced variation. Finally, in this context, Leigh (2004) has shown that in primates, brain growth is an extremely complicated phenomenon and that adult brain size alone is not well associated with dental maturation or with the length of the juvenile growth period (and see Braga and Heuze 2007).

Age profiles of more recent fossil hominin accumulations are not very different from those of living peoples, for example, the skeletal series of Natufians (the pre- or incipient agricultural groups of the Levant) analyzed by Karasik et al. (2000). In this study, using a traditional comparative series as the standard, the mean age at death was 31.5 years; in contrast, applying aging standards derived from local Sinai Bedouins produced a mean age at death of 36.5 years. Very few individuals were placed in the older adult category of 45–50 years of age. Unfortunately, the fossil record of earlier phases of human evolution, with fragmentary, incomplete bones of few individuals generally deriving from many generations, cannot be subjected to this sort of critical comparative study.

Probably the best studied fossil assemblages for which paleodemographic profiles have been developed are those from Krapina and Atapuerca (SH). Each site contains a large number of individuals: for Krapina, between 75 and 92 (Wolpoff 1999), and at Atapuerca, a minimum of 32 individuals (Bermudez de Castro and Nicolas 1997). As mentioned previously, both sites have been interpreted as possessing assemblages indicative of a catastrophic event. This idea for the accumulation of the sample at Krapina was supported by White (2000) and Trinkaus (1985) but criticized by Russell (1987a, b). At Atapuerca, Bermudez de Castro and Nicolas (1997) have argued against the possible catastrophic event proposed by Bocquet-Appel and Arsuaga (1999). Age estimations based on tooth development and emergence and occlusal wear, the elements usually examined in deriving age-at-death determinations in fossil hominins, resulted in a relatively low average age at death at both sites. Profiles from both Atapuerca and Krapina reveal an age-at-death distribution with high adolescent and young adult mortality and a death of older individuals. In an extensive examination of Neanderthal paleodemography, using 206 European and Middle Eastern Neanderthal remains and comparisons to 11 modern human populations including gathering and hunting peoples, agricultural peoples, and archaeological collections, Trinkaus (1995) concluded that Neanderthal populations were under extensive environmental stress that resulted in a unique population profile. The elements of this profile included high levels of infant mortality extending into young adulthood, with few or no individuals surviving into older age categories (+40 years). This latter feature of the Neanderthal mortality profile is unique among all the modern human populations used in his analysis, including archaeological samples. Trinkaus (1995) considers other explanations for this mortality pattern and attempts to minimize the effect of the Krapina and Vindija samples on the resultant profile. These two Croatian sites account for the bulk of adolescent specimens in the overall Neanderthal sample, emphasizing the possibility of alternative explanations for the unusual mortality profiles represented at these sites.

If the Middle Pleistocene Atapuerca (SH) site and the Late Pleistocene analyses by Trinkaus (1995) for Neanderthals are acceptable, using life tables from modern human populations it would not appear possible for these extinct hominins to replace their numbers in each subsequent generation. In another study, Trinkaus and Thompson (1987) concluded that there were no older individuals in Neanderthal populations. This leaves us in the perplexing situation of having to explain why, if these death assemblages are representative of living populations, these hominins did not become extinct after just a few generations. Clearly something is wrong with these analyses. In this context, Ogilvie et al. (1989) concluded that dental enamel hypoplasia indicates that Neanderthals sustained continuing stress from weaning to adulthood, resulting from an inadequacy of foraging technique. One major problem with this analysis is the “osteological paradox” (Wood et al. 1994) in which high frequencies of stress indicators on the skeleton are actually an indication of the adequacy of cultural and/or biological mechanisms in the individuals and populations at risk, in buffering the negative environmental effects.

For Middle and Upper Pleistocene hominin samples, such as those from Atapuerca (SH) and the European Neanderthals, it might be possible to use life history parameters that have been described for modern humans (but see Dean et al. 1986; Bermudez de Castro et al. 2001; Ramirez Rozzi and Bermudez de Castro 2004). For earlier hominins, the issue is very controversial. Caspari and Lee (2004) attempted to circumvent the problems associated with life history differences in human evolution by using dental attributes to grossly divide the hominin fossil record (including members of *Australopithecus*) into younger and older age categories, pointing out that this division will reasonably apply to all the taxa, regardless of possible differences in growth and development.

Determining the Sex of Skeletal Materials

There are also significant limitations in the identification of the sex of a skeleton. How applicable to extinct hominins are the anatomical criteria developed on modern human samples for determining the sex of individual specimens? In general, the sex determination of earlier hominins is based on the anatomy of the os coxae and on comparisons of the level of robusticity of the preserved postcranial bones in the sample. In the case of pelvic bones, unambiguous identification is often impossible, even when the bones are relatively complete and undistorted (Rosenberg 1988). Gracilization related to evolutionary change in fossil samples over time can confound the recognition of sex differences based on skeletal robusticity. For example, the locus H mandible from the Lower Cave, Zhoukoudian, has been identified as a female in comparison with other mandibular specimens. However, it is possible that this Locus was deposited later in time than the other fossil bearing loci, and the more gracile nature of this fossil may be indicative of a male from a later time (Mann 1981).

The clear implication of these problems is that the recognition of sexual dimorphism within an extinct hominin species can be very difficult. Plavcan and Cope (2001) have attempted to determine the validity of species in the fossil record using metric criteria and sample variation. Other researchers have also examined this problem (Lockwood et al. 1996, 2000; Rehg and Leigh 1999), and much of this literature has recently been reviewed by Scott and Lockwood (2004). More broadly, Plavcan (2001) has reviewed the pattern of sexual dimorphism in primates. These studies consider the evidence for the presence of a range of variation that can be reasonably accommodated within a valid species; within such metrically defined species, sex differences are established along the continuum. Ultimately, however, since sample sizes of earlier hominins are very small, both sexes are often collapsed into one. As a consequence of this, the determination of sex in hominin fossil paleodemography has attracted less attention than the establishment of criteria associated with aging.

However, the identification of the sex of fossil skeletal materials can yield significant data on population structure. This is because knowledge of female mortality is crucial to understanding patterns of fertility. Using comparative data from chimpanzees and modern humans groups, Lovejoy (1981) hypothesized a demographic transition at the origin of the hominin lineage, primarily based on decreasing birth intervals. Dall and Boyd (2004) have suggested that lactation in mammals probably evolved as a way to minimize the impact of fluctuations in food resources. Austin et al. (2013) assessed weaning patterns in a sample of modern human and macaque children as a comparative sample to a juvenile Neanderthal specimen. A demographic shift in age at weaning to the time frame of the early evolution of the genus *Homo* is proposed by Kennedy (2005). Thus, a decrease in time spent in lactation and its subsequent effect on birth interval may have been associated with a relatively more consistent food supply in human evolution. Birth interval, age at menarche, and age at first birth (first parity) are highly variable in both chimpanzees and humans (Eveleth and Tanner 1990). Sugiyama (2004b) summarized data on chimpanzees which showed that captive animals display reduced times in each of those categories associated with fertility; in contrast, fertility patterns among wild chimpanzees are quite varied.

Although sexing the skeleton is relatively easy in strongly dimorphic species, the process in modern human populations is much more difficult. Populations and species have varied degrees of dimorphism, and it can be expressed in different ways. White (2000), in a summary of the techniques used to sex the skeleton in recent archaeological populations, recommends seriating the specimens and then determining the most appropriate features within that population to use as sexing criteria. Both White (2000) and Meindl and Russell (1998) provide detailed reviews of the extensive literature on the identification of the sex of skeletal materials. A somewhat different review of the pre-1980 literature is provided in the summary of the Workshop of European Anthropological Association, published in the Journal of Human Evolution (1980).

In earlier, nonmodern hominins, the presence and extent of dimorphism is difficult to understand and quantify. Frayer and Wolpoff (1985) described various models for the identification and comprehension of sexual dimorphism in human evolution. More recent research has generated new models for understanding the context of dimorphism across the hominin lineage and among vertebrates in general. For example, if late secondary sex characteristics are primarily influenced by the production of testosterone, then an understanding of reduced dimorphism in hominins might be explained by a selection model directed toward a decrease in testosterone production or changes in its target cells. Thus, the immune suppression effect of testosterone production is reduced, influencing longevity, and the role of fathers in caregiving might have increased as male–male competition based on testosterone levels was reduced (Wingfield et al. 1997). This is a plausible explanation for reduction of sexual dimorphism and provides an explanation for the evolutionary role of monogamy in human evolution.

In general, however, the study of the regulation and evolution of sexually dimorphic characteristics from a physiological and genetic perspective is just beginning. It is reasonable to infer that some combination of hormonal and genetic factors plays an important role. For example, Skuse (1999) proposed a mechanism of genomic imprinting of the X chromosome as a possible mechanism, and Haqq and Donahoe (1998) reviewed the literature on individuals diagnosed with sexual ambiguity to construct a more holistic model of the factors contributing to the attribution of sex. Significant differences exist in the brains of human males and females, and sex differences are present in many biological systems (Maguire et al. 1999; Goldstein et al. 2001; Allen et al. 2003; Dubb et al. 2003; Raz et al. 2004;

Shah et al. 2004; Vawter et al. 2004). Bolnick and Doebeli (2003) proposed a possible role of sexual selection and sexual dimorphism under conditions of ecological destabilization. The multiple outcomes of this theoretical model seem to indicate that there is a conflict between speciation and dimorphism, i.e., sexual selection for increased dimorphism reduces the possibility of speciation. In this model, under conditions of changing ecological landscapes during the course of human evolution, some species undergo an adaptive speciation while others evolve alternatives to speciation, including an increase in sexual dimorphism. This may be a useful explanatory factor in the differing levels of sexual dimorphism observed in hominin taxa.

For the most part, although sexing is critical to almost all types of skeletal analysis, our ability to apply this to extinct members of the hominin lineage is difficult. Since the number of skeletons present in any analysis of the life history or paleodemography of fossil hominin samples is so small, it makes sense to pool both the male and female skeletons and consider them as a single sample.

Among the confounding difficulties which have led to the pooling of samples is the inability to distinguish dimorphic characteristics among the earliest hominins (including *Australopithecus*). Numerous arguments focused on the evolution of sex differences in the pelvis and in other features related to dimorphism (i.e., female vs. male stature). Assuming the obstetrical dilemma in human evolution, and without knowledge as to the exact time frame when this would have occurred in human biological history, research has pointed to possible evolutionary mechanisms responsible for these differences including sexual selection for more fecund female mates. Guegan et al. (2000) presented data on populations in 38 countries to show that stature dimorphism in females in modern populations could be correlated with complications associated with pregnancy and the birthing process. Nettle (2002) has shown that female height is correlated with reproductive success but that maximum success occurred in females who were below the mean for height. Integrating the data from both of these studies suggests that over time, female height may be more conservative than male height. Thus, differences in dimorphism in human evolution may be related in large measure to variations in males, with female biology remaining somewhat stable. Studies of living humans appear to show that females are less vulnerable to environmental influences on growth processes than males (Stini 1985).

Sexual selection has also been implicated in the evolution of body dimorphism. For example, Pawlowski and Grabarczyk (2003) have argued that the low center of gravity in females, manifest after puberty and adaptive for both pregnancy and the carrying of infants, is the result of sexual selection by males for this specific female body form.

The os coxa is the single most dimorphic feature of humans and, according to Tague and Lovejoy (1986), probably has been for at least the last few million years. The anatomy of the known sample of hominin pelvic bones appears to be related to the conflicting needs of both efficient bipedality and the problems associated with birthing relatively large-brained babies with broad shoulders. It appears that some of the dimorphism present in adult pelvises might actually be present in utero

(Holcomb and Konigsberg 1995). In addition, it is possible that geographic population affects the expression of sexual dimorphism in the pelvis (Patriquin et al. 2003). In modern populations, the accuracy of the assignation of sex using the pelvis is close to 95 % (Murail et al. 1999; Bruzek 2002). According to Leutenegger (1982), all primate females possess a greater ischiopubic index than males do.

Although biases exist in the determination of sex based on features of the skull, there appear to be differential differences between the preservation of female versus male skeletons (Walker et al. 1988). There is a tendency to identify older female skulls as male (see Henke 1974). This is no doubt a direct consequence that the skull becomes more “masculine” as it ages (Meindl et al. 1985); it is difficult, however, to know if this bias applies to fossil hominin studies. Susanne et al. (1985) present data on age changes in cephalic dimensions.

The distinctive features of the male and female os coxae are universal in living humans (and probably most extinct species as well), although there might be some variation in the degree of expression of the differences within these populations. The same, however, does not apply to other characteristics used in sexing the skeleton. Thus, in concert with the techniques applied to determining the age at death of a skeleton, sexing techniques must be population specific. This can be accomplished either through analysis based on the data accumulated on a reference sample of known sex (Steyn and Iscan 1997; Graw et al. 1999; Mall et al. 2000; Asala 2001; Schiwy-Bochat 2001; Pettenati-Soubayroux et al. 2002; Bidmos and Asala 2004) or through seriation of a group of unknown specimens (White 2000) and the application of a variety of statistical techniques to the data. Safont et al. (2000) have employed this method on a modern human sample. Since it can generally be assumed that an unknown sample contains both male and female skeletons, it is reasonable to sort the skeletal elements into male and female categories.

In fossil hominin studies, in contrast, because it is not possible to derive a set of metric or nonmetric characteristics associated with sex (or age for that matter) on an applicable reference sample, it is necessary to derive a set a parameters that best describes (statistically or with other methods) the variation in the sample being examined. Depending on its place in the hominin timescale, comparisons can be made to hominoids, especially chimpanzees, or to living human populations.

An example of this type of analysis was that of Reno et al. (2003) on a fossil sample from Afar Locality (A.L.) 333 and assigned to *A. afarensis* (see also the commentary by Larson 2003). Since the A.L. 333 locale is considered on geological grounds to be a simultaneous death assemblage, it was assumed that the fossil sample represented males and females of the same species. Simulations were undertaken to compare the Afar fossils to modern humans, chimpanzees, and gorillas. Using measurements of postcranial elements, *A. afarensis* was found to be closest to *H. sapiens* in degree of sexual dimorphism (with *H. sapiens* intermediate between the monomorphism of chimps and the extreme dimorphism of *Gorilla* in postcranial dimensions). These researchers also question the simple extrapolation of dimorphism to social categories in primates. They emphasized the striking dissimilarity in sexual dimorphism between canine tooth maturation in chimpanzees and their almost negligible postcranial dimorphism. They conclude that *A. afarensis* possessed a very distinct pattern from polygamous chimpanzees. In this analysis, monogamy is probably the most likely pattern of social organization among these early fossil hominins. Richmond and Jungers (1995) and Lockwood et al. (1996, 2000) have also investigated the pattern of sexual dimorphism in *A. afarensis*. Examinations of sexual dimorphism have been performed on *A. (P.) boisei* specimens (Silverman et al. 2001), face dimorphism in *A. africanus* (Lockwood 1999), sexual dimorphism in *Australopithecus* (*P.) robustus* and early *Homo* (Susman et al. 2001), and the mandibular metrics of a comparative sample of *H. sapiens*, *Pan troglodytes*, *Pongo pygmaeus pygmaeus*, and *Gorilla gorilla gorilla* (Humphrey et al. 1999).

One of the most extensive investigations of sex assignation in a specific sample was undertaken by Bermudez de Castro and Nicolas (1997) on the fossil materials from the Spanish site of Atapuerca (SH). A total sample of 32 individuals was examined, with a 1:1 sex ratio derived from the specimens that could be sexed. They report an overrepresentation of females in the age category between 16 and 20 years. This may be a reflection of a high female mortality in early child bearing years. Additional studies on this collection have been done by Rosas et al. (2002) and Bermudez de Castro et al. (2001), who examined the level of sexual dimorphism in the sample as revealed in mandibular and dental measurements, respectively. Bermudez de Castro et al. (2001) concluded that the dentition showed greater sexual dimorphism than that found in modern humans. In the mandible, sexual dimorphic patterns were present but differed from those in modern humans. Arsuaga et al. (1997) looked at body size and cranial capacity dimorphism, reporting a degree of dimorphism similar to other Middle Pleistocene hominins and modern humans.

Wolpoff (1999) noted that sexual dimorphic characteristics, including overall cranial size and capacity, vault thickness, superstructures and toruses (mastoid process, sagittal keel, nuchal torus), forehead curvature, and functionally related features of facial size and robustness, vary in expression in recent human geographic populations and are a reflection of the hominin evolutionary past in each region. On the basis of these observations, Wolpoff (1999) identified male and female sex differences in an extensive sample of Middle and Upper Pleistocene hominins. Weidenreich's (1935, 1943) detailed studies of the morphology of the *H. erectus* sample from Zhoukoudian suggested a relatively low level of sexual dimorphism, a conclusion that was also found by Mann (1981), who studied the virtually complete Zhoukoudian cast collection.

Other studies of the application of techniques of sexing to fossil hominin materials include the work of Coqueugniot et al. (2000) as well as the application of mandibular ramus posterior flexure to a sample of Neanderthals and early modern humans (Loth and Henneberg 1996), dimorphism in chin morphology in the specimens from Klasies River Mouth (Lam et al. 1996), and an analysis of the Kebara 2 pelvis using various bony dimensions (Tague 1992). Finally, Trinkaus (1980) employed indices of robusticity of postcranial elements to show that European and Near Eastern Neanderthal limb bones show the same degree of sexual dimorphism as modern humans in this feature. In a recent article by Lordkipanidze et al. (2013), the sample of 5 crania from the 1.8-million-year-old site of Dmanisi was divided into male and female based on robusticity of cranial elements.

Other Paleodemographic Parameters

Life History

Life history variables (chapters "▶ Primate Life Histories," Vol. 2 and "▶ Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1), including brain and body size, neonatal weight, length of gestation, lifespan, age of sexual maturation, and age of weaning, are all correlated to each other; various theories have been proposed to explain the evolutionary mechanisms through which this occurs. Using data on living primates, Harvey and Clutton-Brock (1985) noted that the distinctive features of this mammalian order are large brains, prolonged maturation, and long lifespans. Understanding the relationships of these variables to each other from an evolutionary perspective has been the subject of numerous projects and debates (Borries et al. 2013). Pereira (1993) has summarized this work, including a discussion of allometric or correlation analysis. Heterochrony has also been used to explain life history developmental processes that may have characterized human evolution (Gould 1977; Minugh-Purvis and McNamara 2002). The usefulness of heterochrony has been critically evaluated by Godfrey and Sutherland (1996) and Shea (1989).

Gage (1998) compiled all known mortality and fertility data on a broad group of primates. He concluded that a comparison of human and chimpanzees life histories indicates that delayed maturation is a characteristic of humans, whereas an extension of the overall time frame of reproduction, along with an increase in the calculated rate of aging, appears characteristic of chimpanzees. Chimpanzee character state of life history is evolutionarily derived and thus does not make a useful model for understanding the last common ancestor of chimpanzees and humans (see discussions in Duda and Zrzavy 2013). Although this observation must be kept in mind, chimpanzees are our closest living relative; the use of the growing body of literature on chimpanzee studies, especially in the wild, can reasonably provide a point of comparison not only to living humans but also to extinct members of the human lineage. The human life history pattern as described by Smith and Tompkins (1995, p. 260) is that "humans take about twice as long to erupt teeth, twice as long to reach adulthood, and live about twice as long as great apes." This probably represents an overstatement of the unique position of humans within the Primate Order. For example, the work of Zihlman et al. (2004) shows that wild chimpanzees take upward of 3 years longer to mature than animals in captivity. Using M1 eruption times as a proxy for other maturational events, chimpanzees now appear to overlap the range of modern humans. Recent work on sexual maturation of chimpanzees in the wild shows that some groups do not mature until 14 years of age (Sugiyama 2004b).

A comprehensive description of life history in mammals was analyzed using an energetics model by Hill and Kaplan (1999), and an evolutionary model of longevity increases was presented by Carey and Judge (2001). Using game theory, Brommer (2000) also discussed the evolution of life history using the evolutionary concept of fitness. Using seven anthropoid primate species, Leigh (2004) has shown that life history among the primates cannot be related solely to brain size but more specifically to the point in life history in which brain growth occurs. The correlation of diet to primate life history has been addressed by Godfrey et al. (2001) and Kaplan et al. (2000). Day et al. (2002) associated life history variables across various species of animals with the level of predator pressure. Bolnick and Doebeli (2003) have also proposed that species confronted with ecological instability adapt in a number of ways, including changes in sexual dimorphism, speciation, or an alteration of ontogenetic processes that reduces the influence of the destabilizing ecological events. It is possible that some and all combinations of these outcomes have occurred in human evolution. Of critical importance is the plausible role of ontogenetic changes as an adaptive feature in at least some species in human evolution. If, for example, *A. afarensis* does indeed show little sexual dimorphism and, by extrapolation from primate models, this indicates a pattern of monogamy among these hominins, then it is indeed possible that altricial young were also part of this pattern, further supporting Lovejoy's (1981) hypothesis.

Since life history theory is built on the foundation of living animals, it becomes a challenge to integrate fossil hominin species into these analyses. It has been argued that correlations of brain and body size to life history variables supersede any possible analysis of the fossil materials and that all data must be interpreted in this context. Certainly, evolutionary events have produced unique combinations of life history features in the past; and if it is possible to integrate these into the correlation studies, it might serve to more fully represent the life history of hominins across time and space. There appears to be no consensus as to when in the course of hominin evolution modern humanlike life histories evolved. Various perspectives on the evolution of life history have been presented (Smith and Tompkins 1995; Tillier 1995; Bogin 1999; Minugh-Purvis and McNamara 2002; Thompson et al. 2003). More recently Robson and Wood (2008) presented a synthesis of life history data from the fossil record of human evolution and concluded that in the time frame of *Homo heidelbergensis* (viewed by some as archaic *Homo sapiens*), the basic life history parameters similar to modern humans were attained.

In order to reconstruct the life history patterns of earlier hominins, most research has concentrated on the examination of those biological patterns that may yield data documenting rates of maturation. Overwhelmingly, this has meant focusing on the developing dentition with the assumption that the maturation of dental hard tissues and the sequential eruption of the teeth are under strong genetic control, with a minimum of possible environmental influence. Unlike bone, which is subject to remodeling throughout life, dental enamel appears to be relatively stable, preserving the initial structures. Most research on the maturation patterns of earlier hominins focuses either on the pattern and sequential eruption of the developing dentition or on the examination of dental microstructures as time-dependent features. Comparisons between fossil hominins are most usually made to the living great apes, especially chimpanzees, and to modern humans.

Patterns of Maturation

Chimpanzees and humans are characterized by different life history strategies; this should be apparent in the dental calcification and eruption schedules of the two species. What if any pattern differences have been described? The most prominent is that chimpanzees have an accelerated development and eruption of the M1 especially in relationship to the development of I1 (Smith 1994, 2000; critique by Mann et al. 1990). It has also been observed that chimpanzees have a time overlap in the calcification schedule of the molar sequence (Anemone 2002). And finally, chimpanzees have a significant difference in the pattern of calcification and eruption of the permanent canines. Since this tooth is so functionally and anatomically distinct from that of humans, the canine is probably not a good indicator of life history pattern differences (Lampl et al. 1993).

Various models have been used to explain these differences. These include differences in life history (see, e.g., Smith 2000 and the critique by Lampl et al. 2000), but other explanations have been proposed (Simpson et al. 1990; Simpson and Kunos 1998).

Many scholars have undertaken general discussions of how dental development of fossil hominin samples can be understood as part of life history (Bogin 1999; Smith and Tompkins 1995; Bogin and Smith 1996; Kuykendall 2003). Discussions of life history in the early phases of human evolution have been extensively discussed (Dean 1985; Smith 1994; Conroy and Vannier 1989; Mann et al. 1987; Conroy 1988; Mann 1988; Wolpoff et al. 1988; Conroy and Kuykendall 1995; Smith and Tompkins 1995; Clegg and Aiello 1999; Dean et al. 2001; Moggi-Cecchi 2001). Many investigations have also focused on the later phases of human evolution (summarized in Robson and Wood 2008).

Dental Microstructure

Some researchers have maintained that dental enamel and dentin microstructures are useful tools for the reconstruction of the timing of dental development. Dental microstructure is a hard tissue relic of the ontogenetic processes that govern tooth growth (Ramirez Rozzi and Bermudez de Castro 2004; Guatelli-Steinberg et al. 2005). Conversely, it is also possible that these structures reflect a microworld of minianatomical detail that may or may not be useful in the timing of dental development or the reconstruction of phylogenetic relationships.

Bromage and Dean (1985) presented data to support the idea that the timing of tooth development in fossil hominins could be estimated using microstructural details of enamel. Since then there has been much debate about the applicability of these hard tissues to understanding of the times of maturational events in earlier hominins (Dean and Reid 2001; Moggi-Cecchi 2001; Ramirez Rozzi and Bermudez de Castro 2004; Guatelli-Steinberg et al. 2005; Monge et al. 2006; Smith et al. 2010).

Finally, growth and development studies have been undertaken on the femur (Tardieu 1998) and pelvis (Berge 1995) of fossil hominins. In both these studies, although a humanlike pattern of growth best describes all members of the genus *Homo*, australopithecine-grade hominins probably had growth trajectories similar to those in chimpanzees.

What can be concluded from this diverse body of research? Even where a virtually complete skeleton of a youngster (KNM-WT 15000) has been recovered, it has been difficult to reach a consensus about its rate of maturation and its age at death (Clegg and Aiello 1999). The diversity of research on the patterns of maturation in earlier hominins is well illustrated in the edited volume, Patterns of Growth and Development in the Genus *Homo* (Thompson et al. 2003). Thus, it remains very difficult to compare the work presented by one researcher with that of another because the fossil samples and the techniques of analysis that are employed are often so different.

However, and with some reservations, the research results appear to support the general recognition that, by the appearance of members of the genus *Homo*, there was a maturational shift to a more modern humanlike pattern, although that pattern might be manifested in slightly different ways in individual species within *Homo*. If this cautious conclusion continues to be supported by additional data, it will justify the use of the growth and development patterns of modern humans as reference data and for use in modeling population parameters within paleodemographic reconstructions. What sorts of patterns characterized the maturation of the still earlier members of the hominin lineage remains uncertain. However, recent information documenting significant variation in maturational events in both modern humans and chimpanzees suggests that the traditional notion of a uniquely human prolonged period of maturation may have to be reconsidered.

Conclusions

1. The paleodemography of extinct hominin taxa has not produced a corpus of dependable data, and it remains possible that reasonable population-based demographic parameters from fossil assemblages will remain unattainable into the foreseeable future. The use of modeling from archaeological samples holds more promise in an application to the more distant past to capture demographic parameters in long extinct populations in the hominin lineage (Konigsberg and Frankenberg 2013).
2. In contrast, life history reconstruction, establishing some basic parameters associated with demographic analysis, is a more achievable goal. Among these parameters are potential life expectancy, time of maturation, and age at weaning. The accumulation of additional information on living primates has made the simple association of life history variables with gross size variables (e.g., brain size and body size) increasingly untenable.
3. The larger the database on captive and wild chimpanzees, the more difficult it becomes to clearly distinguish their life history variables from those of living

humans. This will certainly affect our interpretations of life history and extrapolations to demographic features that characterize fossil hominin species. Similarly, the more knowledge we have of the extent of modern human variation and plasticity, the more difficult it becomes to specifically categorize unique autapomorphic features of human life history.

4. Culture (in conjunction with significant developmental plasticity) may be more important as regard understanding human life history than biology, especially in variations in the expression of features such as longevity and age at weaning, and perhaps even maturation rates, general reduction in the age of first menstruation, and others. Such factors may better explain the large ranges of variation that have been observed in both humans and chimpanzees.

In sum, we know very little of the demography including all aspects of population parameters of earlier members of the hominin lineage, and much that appears to be understood requires reevaluation on the basis of newly acquired data from nonhuman primates and the increasing comprehension of the range of variation characterizing human growth and maturation.

Cross-References

▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
▶ Estimation of Basic Life History Data of Fossil Hominoids
▶ Modeling the Past: Archaeology
▶ Modeling the Past: The Primatological Approach
▶ Primate Life Histories
▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology

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Hominin Paleodiets: The Contribution of Stable Isotopes

Matt Sponheimer and Julia Lee-Thorp

Contents

Abstract

Stable isotope ratio analysis is now regularly used to investigate early hominin diets based upon the principle that 'you are what you eat'. Analysis of collagen from Neanderthals and anatomically modern humans prior to 20 Ka has shown them to be significantly enriched in ^{15}N compared to contemporaneous carnivores and herbivores. This suggests that much of their dietary protein, although not necessarily their dietary energy, came from animal foods. Carbon isotope

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M. Sponheimer (✉)
Department of Anthropology, University of Colorado at Boulder, Boulder, CO, USA
e-mail: sponcu@gmail.com; matt.sponheimer@colorado.edu

J. Lee-Thorp
Research Laboratory for Archaeology and the History of Art, University of Oxford, Oxford, UK
e-mail: julia.lee-thorp@rlaha.ox.ac.uk

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analysis of the enamel mineral of southern African australopiths and early *Homo* has revealed that these taxa consumed $\sim$30 % C$_4$ foods such as tropical grasses, sedges, or animals that ate these foods. Moreover, the australopiths are characterized by remarkably variable δ^{13}C values. Chimpanzees, in contrast, are nearly pure C$_3$ consumers even in environments with abundant C$_4$ vegetation. These data suggest that when confronted with increasingly open areas, chimpanzees continue to exploit the foods that are most abundant in forest environments, whereas southern African australopiths utilized novel C$_4$ resources in addition to forest foods. However, new data from eastern and central Africa show that not all australopiths follow this pattern. The earliest australopiths had nearly pure C$_3$ diets, but by about 2 Ma others ate predominantly C$_4$ vegetation. It also appears that increased masticatory robusticity in the australopiths is associated with greater C$_4$ consumption.

Introduction

The nature of early hominin diets has been the subject of lively debate and not without good reason (e.g., Dart 1957; Robinson 1954; Jolly 1970; Brain 1981; Binford 1981; Grine and Kay 1988; Sillen 1992; Stiner 1994; Lee-Thorp et al. 1994; Sponheimer and Lee-Thorp 1999; Richards et al. 2000; Speth and Tchernov 2001). Most large primates spend at least 50 % of their waking hours searching for or consuming food (e.g., Altmann and Altman 1970; Teleki 1981; Goodall 1986; see chapters "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition," "▶ Great Ape Social Systems," and "▶ The Biotic Environments of the Late Miocene Hominoids Vol. 2). Thus, if we seek to know what "a day in the life" of our ancestors was like, understanding what they ate would represent an enormous step in that direction (see chapter "▶ Dental Adaptations of African Apes," Vol. 2). Furthermore, diet is considered among the most important factors underlying behavioral and ecological differences among extant primates (Ungar 1998; Fleagle 1999), and thus the story of our ancestors' evolving diets is likely to be intertwined with that of how our species, *Homo sapiens*, came to be. We can glean paleodietary information from many sources (see chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). Archaeological evidence in the form of stone tools and butchered animal bones is one source of dietary information, which tells us about the kinds of animals that hominins utilized as well as their procurement strategies (e.g., Binford 1981; Brain 1981; Blumenschine 1987; Stiner 1994; Speth and Tchernov 2001). Yet, such evidence tends to overemphasize the importance of animal foods at the expense of plant foods that make up the bulk of most primate diets (e.g., Lee 1979; Eaton and Konner 1985; Milton 2002). Moreover, the first potential hominins (Senut et al. 2001; Brunet et al. 2002; Haile-Selassie et al. 2004) precede the earliest archaeological traces by millions of years (Semaw et al. 1997; de Heinzelin et al. 1999), and thus the archaeological record remains silent with regard to the diets of the earliest hominins (see chapters "▶ Modeling the Past: Archaeology," Vol. 1 and "▶ Overview of Paleolithic Archaeology," Vol. 3).

As a result, paleoanthropologists have had to look for other sources of paleodietary information. Dental allometry/morphology and microwear have received much attention and provided important insights into the diets of our ancestors (see chapters "▶ Hominoid Cranial Diversity and Adaptation" and "▶ Dental Adaptations of African Apes," Vol. 2; Robinson 1954; Grine 1981, 1986; Grine and Kay 1988; Ungar and Grine 1991; Teaford et al. 2002; Ungar 2004). Still, these techniques have limitations. For instance, the relatively large incisors and bunodont molars of modern *Papio* suggest a frugivorous diet (Hylander 1975; Fleagle 1999; Ungar 1998), and yet many *Papio* populations consume large quantities of grasses, for which they have no apparent dental specializations (Altmann and Altman 1970; Harding 1976; Dunbar 1983; Strum 1987). Ungar (2004) has also argued that the dental morphology of extant apes and early hominins may tell us more about their fallback foods than it does about their "typical" diets. Dental microwear, in turn, reveals a great deal about the mechanical properties of a primate's food. Primates that eat hard, brittle foods, such as gray-cheeked mangabeys (*Lophocebus albigena*), have relatively more microscopic pitting on their molars than do those that eat more pliant, tough foods like mountain gorillas (*Gorilla gorilla beringei*) (Grine and Kay 1988; Ungar 1998). However, microwear is quickly obliterated and therefore provides dietary information for a few brief days, which may or may not be representative of an individual's "average" diet. In addition, soft foods, such as animal flesh, may not always produce recognizable microwear signatures. Thus, even with these important techniques in our paleodietary arsenal, a great deal about the diets of early hominins remains unknown.

Consequently, new paleodietary techniques have emerged in recent years, one of the most important of which is stable isotope analysis. The idea behind this technique is that "you are what you eat." In other words, the isotopic composition of one's food is ultimately traceable in one's tissues. Thus, stable isotope analysis provides a direct chemical means of investigating the diets of modern and fossil primates. In this paper, we address the contribution of stable isotope analysis to our understanding of early hominin diets. The paper is divided roughly into two sections: stable isotope analysis of bone and dentine collagen, which has been used to investigate the diets of our close cousins the Neanderthals and early modern humans (Bocherens et al. 1991, 1999, 2001, 2005; Fizet et al. 1995; Richards et al. 2000, 2001; Pettitt et al. 2003; Schulting et al. 2005), and stable isotope analysis of enamel apatite, which has shed much light on the diets of the South African australopiths and early *Homo* (see chapters "▶ Analyzing Hominin Phylogeny: Cladistic Approach," "▶ The Species and Diversity of Australopiths," and "▶ The Earliest Putative *Homo* Fossils," Vol. 3; Lee-Thorp et al. 1994, 2000; Sponheimer and Lee-Thorp 1999, 2003; van der Merwe et al. 2003; Sponheimer et al. 2005a). We proceed in this reverse chronological order in an effort to trace the general development of paleodietary stable isotope studies: collagen was first utilized in 1977 with enamel apatite studies appearing a decade later. In addition,

Table 1 Specimen numbers, taxon, $\delta^{13}C$, $\delta^{15}N$, and publication date for Neanderthals and anatomically modern humans (The 1991 publication is Bocherens et al. 1991; the 1995 publication is Fizet et al. 1995; the 1999 publication is Bocherens et al. 1999; the 2000 publication is Richards et al. 2000; the 2001a publication is Bocherens et al. 2001; the 2001b publication is Richards et al. 2001; the 2003 publication is Pettitt et al. 2003; the 2005a publication is Bocherens et al. 2005; and the 2005b publication is Schulting et al. 2005))

Specimen	Taxon	$\delta^{13}C$	$\delta^{15}N$	Published
Marillac 9	Neanderthal	−20.2	9.3	1991
Marillac 10	Neanderthal	−19.1	11.6	1995
Scladina 4A-2	Neanderthal	−19.9	10.9	1999
Vindija 207	Neanderthal	−19.5	10.1	2000
Vindija 208	Neanderthal	−20.5	10.8	2000
Scladina 1B-4	Neanderthal	−21.2	11.8	2001a
Engis 2	Neanderthal	−19.6	12.6	2001a
Spy OMO 1	Neanderthal	−19.8	11.0	2001a
Saint-Césaire 1	Neanderthal	−19.8	11.4	2005a
Marillac M70 c10 F10-41	Neanderthal	−19.1	11.5	2005a
Marillac H1	Neanderthal	−19.5	11.4	2005a
Marillac H2	Neanderthal	−21.8	8.4	2005a
Brno-Francouzska 2	AMH	−19.0	12.3	2001b
Dolní Vestoniče 35	AMH	−18.8	12.3	2001b
Kostenki 1	AMH	−18.2	15.3	2001b
Kostenki 18	AMH	−19.1	13.1	2001b
Mal'ta 1	AMH	−18.4	12.2	2001b
Paviland 1	AMH	−18.4	9.3	2001b
Sunghir 1	AMH	−19.2	11.3	2001b
Sunghir 2	AMH	−19.0	11.2	2001b
Sunghir 3	AMH	−18.9	11.3	2001b
Arene Candide 1	AMH	−17.6	12.4	2003
Eel-1	AMH	−19.2	11.2	2005b

the temporally and geographically restricted discussion herein (i.e., the emphasis on European Neanderthals and South African australopiths) is more a reflection of the limited degree to which stable isotopes have been used to investigate the diets of Plio-Pleistocene hominins, than selective presentation on our part. The only data we have excluded for the purpose of this paper are for specimens younger than 20 Ka. The stable isotope data for all older hominins, which we are aware of at least, are discussed herein and can be found in Tables 1 and 2.

Collagen

The first paleodietary study using stable isotopes sought to document maize consumption among Native American populations in New York State (Vogel and van der Merwe 1977). This application was made possible by differences in the photosynthetic pathways of plants. Tropical grasses, such as maize, use C_4

Table 2 Specimens, taxa, proveniences, $\delta^{13}C$ values, and references for South African australopith and early *Homo* specimens

Specimen	Tooth	Taxon	Provenience	$\delta^{13}C$	References
SK1512	P	*Paranthropus robustus*	SK1	−8.8	Lee-Thorp et al. (1994)
SK879	M	*Paranthropus robustus*	SK1	−8.5	Lee-Thorp et al. (1994)
SKX5015	LM_3	*Paranthropus robustus*	SK1	−9.6	Lee-Thorp et al. (1994)
SK878	RP_3	*Paranthropus robustus*	SK1	−6.8	Lee-Thorp et al. (1994)
SK879	M	*Paranthropus robustus*	SK1	−8.1	Lee-Thorp et al. (1994)
SKX1312	LM^1	*Paranthropus robustus*	SK2	−8.1	Lee-Thorp et al. (1994)
SKX333	RM_1	*Paranthropus robustus*	SK2	−10.0	Lee-Thorp et al. (1994)
SKX35025	RM	*Paranthropus robustus*	SK3	−7.9	Lee-Thorp et al. (1994)
SK876	M	*Paranthropus robustus*	SK1	−6.7	Lee-Thorp et al. (2000)
TM 1600	LM_2	*Paranthropus robustus*	KB3	−7.9	Sponheimer et al. (2005a)
SK 19	RM_3	*Paranthropus robustus*	SK1	–6.3	Sponheimer et al. (2005a)
SK 41	LM^3	*Paranthropus robustus*	SK1	−6.7	Sponheimer et al. (2005a)
SK 57	LM^3	*Paranthropus robustus*	SK1	−6.5	Sponheimer et al. (2005a)
SK 14000	LM^3	*Paranthropus robustus*	SK1	−5.9	Sponheimer et al. (2005a)
SK 14132	RM^3	*Paranthropus robustus*	SK1	−6.9	Sponheimer et al. (2005a)
SKW 6	LM^3	*Paranthropus robustus*	SK1	−7.0	Sponheimer et al. (2005a)
SKW 3068	LM^2	*Paranthropus robustus*	SK1	−8.1	Sponheimer et al. (2005a)
SKW 4768	LM^2	*Paranthropus robustus*	SK1	−7.4	Sponheimer et al. (2005a)
MLD 30	RM^1	*Australopithecus africanus*	MAK3	−5.6	Sponheimer and Lee-Thorp (1999a)
MLD 41	M	*Australopithecus africanus*	MAK3	−11.3	Sponheimer and Lee-Thorp (1999a)
MLD12	RM^3	*Australopithecus africanus*	MAK3	−7.7	Sponheimer and Lee-Thorp (1999a)
MLD28	RM^3	*Australopithecus africanus*	MAK3	−8.1	Sponheimer and Lee-Thorp (1999a)
STS 31	RM^3	*Australopithecus africanus*	ST4	−6.8	Sponheimer et al. (2005a)

(*continued*)

Table 2 (continued)

Specimen	Tooth	Taxon	Provenience	$\delta^{13}C$	References
STS 32	RM^3	*Australopithecus africanus*	ST4	−7.8	Sponheimer et al. (2005a)
STS 45	RM^2	*Australopithecus africanus*	ST4	−4.0	Sponheimer et al. (2005a)
STS 72	RM^3	*Australopithecus africanus*	ST4	−9.7	Sponheimer et al. (2005a)
STS 2218	M	*Australopithecus africanus*	ST4	−5.9	Sponheimer et al. (2005a)
STW 73	RM^2	*Australopithecus africanus*	ST4	−8.8	van der Merwe et al. (2003)
STW 276	LM_1	*Australopithecus africanus*	ST4	−8.0	van der Merwe et al. (2003)
STW 252	RM^1	*Australopithecus africanus*	ST4	−7.4	van der Merwe et al. (2003)
STW 211	M	*Australopithecus africanus*	ST4	−7.3	van der Merwe et al. (2003)
STW 304	M	*Australopithecus africanus*	ST4	−7.4	van der Merwe et al. (2003)
STW 14	LM_1	*Australopithecus africanus*	ST4	−6.7	van der Merwe et al. (2003)
STW 315	Ldm_2	*Australopithecus africanus*	ST4	−5.7	van der Merwe et al. (2003)
STW 309b (409)	LM_1	*Australopithecus africanus*	ST4	−6.1	van der Merwe et al. (2003)
STW 229	P	*Australopithecus africanus*	ST4	−5.8	van der Merwe et al. (2003)
STW 303	RM^2	*Australopithecus africanus*	ST4	−4.3	van der Merwe et al. (2003)
STW 236	P	*Australopithecus africanus?*	ST4	−3.7	van der Merwe et al. (2003)
STW 213i	LM_1	*Australopithecus africanus?*	ST4	−1.8	van der Merwe et al. (2003)
STW 207	?	*Australopithecus africanus?*	ST4	−2.0	van der Merwe et al. (2003)
SK 80/847	P	Early *Homo*	SK1	−7.1	Lee-Thorp et al. (2000)
SK 27	LM^3	Early *Homo*	SK1	−8.2	Lee-Thorp et al. (2000)
SK 2635	P	Early *Homo*	SK1	−9.2	Lee-Thorp et al. (2000)

In the provenience column, site abbreviations (*SK* Swartkrans, *MAK* Makapansgat, *ST* Sterkfontein, *KB* Kromdraai B) are followed by the appropriate Member number

photosynthesis, while virtually all other potential plant foods in New York State use C_3 photosynthesis. The C_3 photosynthetic pathway discriminates markedly against ^{13}C, and as a consequence, C_3 plants have very depleted $^{13}C/^{12}C$ ratios. In contrast, plants that utilize the C_4 photosynthetic pathway discriminate less against ^{13}C and

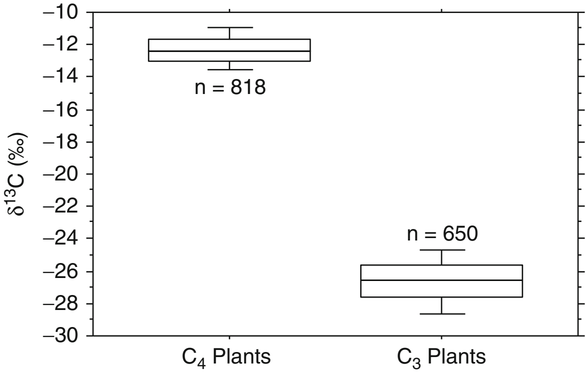


Fig. 1 $^{13}C/^{12}C$ ratios of plants using C_3 (trees, bushes, shrubs, and forbs) and C_4 photosynthesis (grasses and some sedges) in Kruger National Park, South Africa. The boxes represent the 25th–75th percentiles (with the medians as *horizontal lines*), and the whiskers show the 10th–90th percentiles. The carbon isotope compositions of plants using these different photosynthetic pathways are highly distinct. Maize is a tropical grass that uses C_4 photosynthesis, and thus it has a very different carbon isotope composition than other foods that were consumed by Native Americans in New York State (Vogel and van der Merwe 1977)

are consequently relatively enriched in ^{13}C (Smith and Epstein 1971; Fig. 1). These distinct isotopic signatures are passed down into the tissues of individuals that eat these plants. Thus, individuals who eat large quantities of C_4 plants like maize will be relatively enriched in ^{13}C compared to those who eat only C_3 vegetation (see chapters "▶ Role of Environmental Stimuli in Hominid Origins," "▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins," "▶ Analyzing Hominin Phylogeny: Cladistic Approach," and "▶ The Species and Diversity of Australopiths," Vol. 3). Vogel and van der Merwe (1977) analyzed the bone collagen of individuals ranging in age from ~4,000 B.P. to ~500 B.P. They saw little evidence of maize consumption among the oldest individuals but found that maize had become a very important dietary resource by about 1,000 B.P. – sometimes representing up to 50 % of an individual's diet. This study paved the way for a plethora of innovative applications in the following decades which relied on stable isotope abundances in bone collagen (see chapter "▶ Taphonomic and Diagenetic Processes," Vol. 1); however, since collagen is rarely preserved for more than 10,000 years, these investigations were largely confined to the recent past. Yet, it has been shown that, under the right conditions, bone collagen can survive for 200,000 years or more (Jones et al. 2001). Thus, it has proven possible to analyze the bone collagen of late Pleistocene hominins in certain cases.

Collagen: Methodological Considerations

Before proceeding to the hominin data, we will briefly discuss a few relevant methodological considerations. Much has changed since the early days of stable isotope analysis. Today, only small samples are required for analysis, and automation has led to significantly increased sample throughput in labs around the world. Nevertheless, the basic procedures have remained largely the same, even though the protocols vary somewhat from lab to lab. Here, we briefly summarize the operational protocols of the labs that have analyzed the collagen of early hominins. One must keep in mind, however, that this is meant to be a general summary, not an exhaustive step by step explication of analytical procedures.

After surface cleaning, bone or dentine samples are demineralized in diluted HCl (0.5–1.0 M) for periods ranging from 20 min to 5 days. Performing this step at low temperature (5 °C) is one recent innovation that allows collagen to be extracted from very old, fragile samples (Richards and Hedges 1999; Jones et al. 2001). The insoluble residue may then be soaked in 0.125 N NaOH to remove contaminating humic acids; but as this leads to collagen solubilization and decreased extraction yields, it is no longer favored. Fortunately, neglecting this step appears to have little effect on the resulting stable isotope ratios (Bocherens et al. 1999). The residue is then often gelatinized in weak HCl at 75–100 °, filtered, and freeze-dried. A small (~1 mg) sample of this purified collagen is then combusted in an elemental analyzer, and the resultant CO_2 and N_2 gases are analyzed for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ abundances in a stable isotope ratio mass spectrometer. Stable light isotope ratios are expressed as δ values in parts per thousand (‰) relative to international standards, which are PDB (a marine carbonate) and atmospheric N_2 for carbon and nitrogen, respectively. Standard deviations of replicate measurements are generally about ±0.1 ‰ for carbon and ±0.2 ‰ for nitrogen. Importantly, collagen degradation is known to alter stable isotope ratios significantly. To produce reliable results, collagen must generally have a carbon/nitrogen ratio between 2.9 and 3.6, with carbon and nitrogen percentages of at least 15 % and 5 %, respectively (Ambrose 1990).

Our understanding of the relationship between dietary $\delta^{13}C$ and collagen $\delta^{13}C$ has improved significantly since the first use of stable isotopes for paleodietary reconstruction. Experimental studies of rodents on controlled diets have shown that collagen $\delta^{13}C$ is enriched by about +5 ‰ relative to dietary protein (Ambrose and Norr 1993; Tieszen and Fagre 1993), as dietary amino acids are preferentially utilized for tissue synthesis. In contrast, carbon from dietary carbohydrate and lipid makes much less of a contribution to bone collagen (or indeed hair, muscle, etc.). Consequently, bone collagen $\delta^{13}C$ (and $\delta^{15}N$) tells you more about the protein component of an individual's diet than it does about their "whole" or "bulk" diet. This is significant, as animal foods, which are high in protein, will be overrepresented in bone collagen at the expense of low-protein vegetable foods. This bias must be borne in mind when interpreting collagen stable isotope data.

The Neanderthals

Bocherens et al. (1991) performed the first stable isotope analysis of a Neanderthal and associated fauna from the site of Marillac in France. This study demonstrated that enough collagen could be extracted from bones more than 40,000 years old and paved the way for subsequent analyses of Neanderthals from Marillac and Saint-Césaire (Fizet et al. 1995; Bocherens et al. 2005); Scladina Cave, Awirs Cave, and Betche-al-Roche Cave in Belgium (Bocherens et al. 1999, 2001), and Vindija Cave in Croatia (Richards et al. 2000). Virtually all native European plants use the C_3 photosynthetic pathway. As a result, these plants have similar carbon isotope compositions, although those in densely wooded environments are somewhat depleted in ^{13}C due to the canopy effect (Vogel 1978; van der Merwe 1989). Thus, not surprisingly, carbon isotopes revealed little about the diets of Neanderthals, save for the possibility that they utilized few food resources from closed environments (Bocherens et al. 1999; Richards et al. 2000).

The nitrogen isotopes in Neanderthal bone collagen, however, proved more revealing. Nitrogen isotopes ratios ($^{15}N/^{14}N$) are known to increase by about 3 ‰ up every step in the food chain (e.g., Minagawa and Wada 1984; Schoeninger and DeNiro 1984; Ambrose and DeNiro 1986). Thus, within a hypothetical food web, if plants have $\delta^{15}N$ values of 0 ‰, herbivores like reindeers have $\delta^{15}N$ values of about 3 ‰, while carnivores such as wolves have $\delta^{15}N$ values of about 6 ‰. And although nitrogen isotope distributions in food webs are more complicated than this hypothetical example suggests – due to heterogeneity in plant $\delta^{15}N$ and the disparate physiological adaptations and requirements of mammals (Ambrose and DeNiro 1986; Sealy et al. 1987; Sponheimer et al. 2003a) – the general pattern has been shown to be robust in both terrestrial and marine ecosystems. Thus, analysis of nitrogen isotopes in bone collagen can potentially reveal the trophic level at which a hominin was feeding. This is relevant for investigating Neanderthal diets, as their degree of carnivory and manner of carcass acquisition (hunting or scavenging) have been the subject of considerable debate (e.g., Binford 1981; Mellars 1989; Stiner 1994; Speth and Tchernov 2001; see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3).

Intriguingly, all published studies have shown that Neanderthals have very high $\delta^{15}N$, well above that of contemporaneous herbivores such as horses (*Equus caballus*), reindeer (*Rangifer tarandus*), and bison (*Bison priscus*) and similar to that of carnivorous wolves (*Canis lupus*), hyenas (*Crocuta spelaea*), and lions (*Panthera spelaea*) (Bocherens et al. 1991, 1997, 2001, 2005; Fizet et al. 1995; Richards et al. 2000). Indeed, analysis of variance and Fisher's PLSD test of the combined datasets show that Neanderthal $\delta^{15}N$ ($x = 10.9$ ‰, s.d. = 1.1, $n = 12$) is not only significantly higher than herbivore $\delta^{15}N$ ($x = 5.8$ ‰, s.d. = 1.6, $n = 132$) ($P < 0.001$) but also slightly higher than carnivore $\delta^{15}N$ ($x = 9.7$ ‰, s.d. = 1.1, $n = 26$) ($P = 0.02$) (Fig. 2). We should note that the combined dataset contains specimens that accumulated over ~70,000 years and in locations throughout Europe and that such temporal and spatial mixing increases intrataxonomic variability making statistically significant differences between taxa less likely. For instance, Stevens and Hedges (2004) found that European horse (*Equus* spp.) $\delta^{15}N$ fluctuated by at least 4 ‰ over the last 40,000 years due to glacially mediated changes in the nitrogen cycle. Hence, it is particularly striking that significant differences are found between Neanderthals, herbivores, and carnivores without controlling for temporal and spatial variation. In general, the $\delta^{15}N$ data appear to

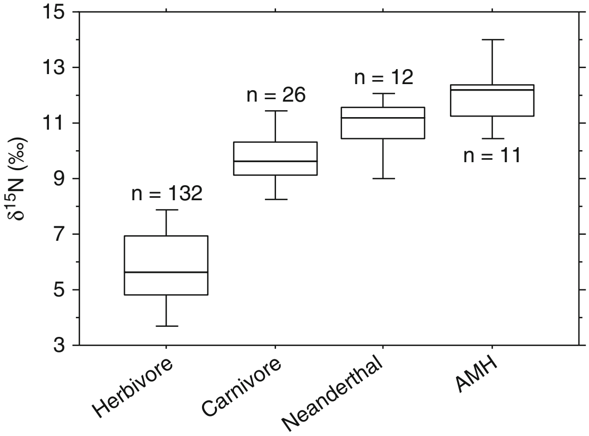


Fig. 2 $\delta^{15}N$ of Neanderthals, mid-Upper Paleolithic humans, herbivores, and carnivores. The boxes represent the 25th–75th percentiles (with the medians as *horizontal lines*) and the whiskers show the 10th–90th percentiles

suggest that Neanderthals received much of their dietary protein from animal foods (Richards et al. 2000). Enrichment in ^{15}N compared to (other) carnivores *may* suggest a dependence on herbivores with relatively high $\delta^{15}N$ such as mammoths (*Mammuthus primigenius*) or even the consumption of omnivorous bears (*Ursus* spp.) (Richards et al. 2000; Bocherens et al. 2001, 2005). While the interpretation of these data remains difficult, it is clear that Neanderthal diets were distinct from those of contemporary herbivorous fauna.

This leads inexorably to the question, "Were Neanderthal diets distinct from those of their hominin contemporaries?" (see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3). While it has not yet been possible to compare the stable isotope compositions of Neanderthals and contemporaneous anatomically modern humans (AMH), Richards et al. (2001) were able to analyze nine near contemporaries from the mid-Upper Paleolithic (~28–20 Ka) at Brno-Francouzská and Dolní Věstonice (Czech Republic); Kostenki, Mal'ta, and Sunghir (Russia); and Paviland (Great Britain). They compared these anatomically modern humans to the five Neanderthals that had been published at the time and argued that the modern humans were even more elevated in $\delta^{15}N$ ($x = 12.0$ ‰, s.d. $= 1.6$, $n = 9$). This suggested that anatomically modern humans were also highly dependent on animal foods. Richards et al. (2001) argued, however, that even the consumption of high $\delta^{15}N$ herbivores like mammoth would not be sufficient to account for the extremely elevated $\delta^{15}N$ of these AMH. Instead, they suggested that these humans had begun to diversify their resource base to include freshwater aquatic resources such as fish and waterfowl, which can be more enriched in ^{15}N than terrestrial resources (Dufour et al. 1999; Katzenberg and Weber 1999). This suggestion was rather surprising, as there is little direct archaeological evidence for exploitation of such foods at this time, although such evidence becomes abundant by the late Upper Paleolithic. Yet, with the subsequent publication of seven new Neanderthal specimens (Bocherens et al. 2001, 2005) and two more mid-Upper Paleolithic humans (Pettitt et al. 2003; Schulting et al. 2005), there is no longer any statistically significant difference in the $\delta^{15}N$ of AMH

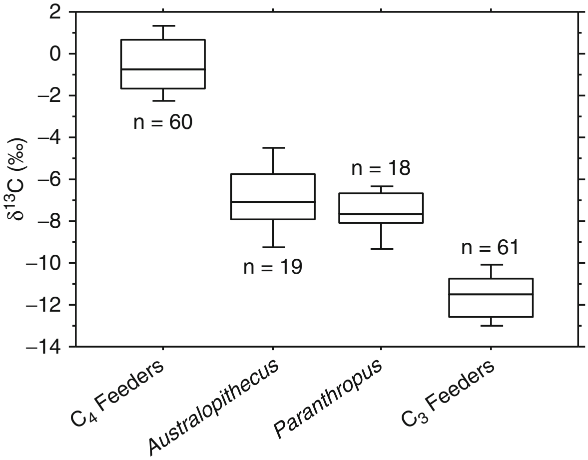


Fig. 3 $\delta^{13}C$ for australopiths, C_3 plant consumers (browsing/frugivorous bovids and giraffids) and C_4 plant consumers (grazing bovids and equids). The boxes represent the 25th–75th percentiles (with the medians as *horizontal lines*) and the whiskers show the 10th–90th percentiles. Given the size of this dataset, there can be no doubt that australopith $\delta^{13}C$ is highly distinct from that of associated browser/frugivores (This figure was produced using data available in 2006. The fully updated dataset is available in Sponheimer et al. (2013))

($x = 11.8$ ‰, s.d $= 1.6$, $n = 11$) and Neanderthals ($P = 0.06$ t-test; $P = 0.09$ Mann-Whitney U) (Fig. 3; Table 1). There is, however, a small but significant difference in the $\delta^{13}C$ of AMH ($x = -18.7$ ‰, s.d. $= 0.5$, $n = 11$) and Neanderthals ($x = -20.0$ ‰, s.d. $= 0.8$, $n = 12$) ($P < 0.01$ t-test and Mann-Whitney U), although the meaning of this difference is unclear. A greater reliance on open area resources such as ^{13}C-enriched reindeer by AMH is one of many possible explanations. More salient from the perspective of dietary breadth, Levene's test reveals no significant differences in the isotopic variability of Neanderthals and AMH ($\delta^{13}C$, $P = 0.23$; $\delta^{15}N$, $P = 0.61$), and thus there is little isotopic support for utilization of novel resources or greater resource breadth in AMH prior to 20 Ka.

These stable isotope studies are an important complement to traditional archaeological paleodietary studies, as they represent a direct measure of the foods that an individual ate that is independent of the taphonomic biases that bedevil faunal analyses (Lyman 1994). Nevertheless, interpretation of these stable isotope data is not straightforward, and there remain a number of important unanswered questions. For instance, why are both hominins enriched by more than 5 ‰ compared to associated herbivores when an enrichment of about 3 ‰ would be expected for a carnivore? Stated otherwise, why is their $\delta^{15}N$ significantly higher than that of associated carnivores? As discussed earlier, this may be partially, but not satisfactorily, explained by the consumption of herbivores with unusually high $\delta^{15}N$ such as mammoths or even by the consumption of omnivores and/or aquatic resources. Another possibility, however, is that there is some physiological explanation for their extremely high $\delta^{15}N$. Experimental studies have shown that when herbivores are fed diets with crude protein contents that are much greater than their nutritional requirements, their diet-tissue spacing can become much greater than 3 ‰ (Sponheimer et al. 2003a). This implies that if the prevailing environment forced Neanderthals to consume high-protein diets that considerably exceeded their crude protein requirements, their diet-tissue spacing might have exceeded 3 ‰, thus artificially increasing their $\delta^{15}N$ compared to other taxa. On the other hand, committed carnivores generally have smaller diet-tissue spacing than herbivores (Robbins et al. 2005). Regardless, the anomalously high $\delta^{15}N$ of mammoths and low $\delta^{15}N$ of cave bears (Bocherens et al. 1997; Ambrose 1998) may also hint at the importance of physiological adaptations in determining an organism's nitrogen isotope composition.

It is worth noting that while such interpretive difficulties exist, they do not diminish the significance of these studies. Even if the Neanderthals did have artificially increased diet-tissue spacing due to a high-protein intake, it might erase their distinctiveness from other carnivores, but would certainly not make them look herbivorous.

Enamel Apatite

Older hominin material is not amenable to this form of analysis as bone collagen is rarely preserved from beyond the late Pleistocene (Jones et al. 2001). However, the carbon isotopes in the bone's mineral component (a biological apatite) can also be used as dietary proxies (Sullivan and Krueger 1981, 1983; Lee-Thorp and van der Merwe 1987). But even though bone mineral clearly persists beyond bone collagen, it can be altered postmortem, often resulting in the loss of the biogenic dietary signal (Schoeninger and DeNiro 1982; Lee-Thorp and van der Merwe 1987; Lee-Thorp 2002). This is due to the bone's high organic content, porosity, and small crystal size, which make it susceptible to dissolution/reprecipitation phenomena and facilitate the incorporation of diagenetic carbonate ions (e.g., LeGeros 1991; Lee-Thorp 2002; Lee-Thorp and Sponheimer 2003). Thus, bioapatite paleodietary studies were forestalled until Lee-Thorp and van der Merwe (1987) showed that dental enamel from ancient fauna with well-understood diets retained its biogenic isotope signal. For example, they showed that fossil equids, like their modern counterparts, had C_4-dominated signatures, while fossil tragelaphines had C_3-dominated signatures like their modern descendants. Since then, numerous empirical and theoretical studies have substantiated this finding (e.g., Lee-Thorp et al. 1989a; Wang and Cerling 1994; Sponheimer and Lee-Thorp 1999b; Hoppe et al. 2003; Lee-Thorp and Sponheimer 2003; Trickett et al. 2003). The enamel's resistance to diagenetic phenomena is conferred by its virtually organic-free and highly-crystalline state (LeGeros 1991), which renders it effectively "prefossilized." Thus, tooth enamel offered the possibility of investigating the diets of early Pleistocene and even Pliocene hominins.

Enamel Bioapatite: Methodological Considerations

For the reasons outlined above, only tooth enamel is sampled for stable isotope analysis of hominin and non-hominin specimens that are millions of years old. Initially, a sample of 200–400 mg was needed (about half of a baboon's molar), but advances in mass spectrometry have reduced the necessary sample size to a few milligrams (Lee-Thorp et al. 1997; Sponheimer 1999). As a result, it has become possible to sample teeth while producing little to no readily observable damage. As a result, more teeth have become available for analysis.

We will now give an overview of the recent sampling and pretreatment protocols, which are modified after Lee-Thorp et al. (1997) and Sponheimer (1999). Specimens are given a careful visual inspection prior to sampling, and those that are heavily stained or have mineral inclusions in the potential sampling areas are excluded from analysis. Generally, only permanent dentition is sampled, with a heavy emphasis on late-forming teeth such as M_2s and M_3s. Powdered enamel samples are acquired (usually from a tooth's buccal surface) using a low-speed rotary drill with a diamond-tipped burr. However, most of the recently sampled hominin teeth had been previously fractured, which allowed sampling between the occlusal surface and the enamel-dentine junction so as to avoid damage to the external surface of the teeth. Although only small samples are taken (~2 mg), we generally attempt to sample over as extensive an area as is possible, so as to obtain enamel formed over a considerable period of time. The enamel powder is soaked for about 10 min in 1.5 % sodium hypochlorite to remove organic contaminants and then rinsed to neutrality. The remaining enamel powder is then pretreated with 0.1 M acetic acid for ~10 min to remove diagenetic carbonates, rinsed to neutrality, and freeze-dried. It is worth noting that these pretreatment protocols can vary from lab to lab, and even within labs over time. As different pretreatments can lead to small but significant differences in a sample's stable isotope composition (especially oxygen), one must compare stable isotope values for the teeth analyzed following different protocols with caution. Finally, each sample is placed in an individual reaction vessel and analyzed for $^{13}C/^{12}C$ and $^{18}O/^{16}O$ using an autocarbonate device coupled to a stable isotope ratio mass spectrometer. Carbon and oxygen isotope ratios are expressed as δ (^{13}C, ^{18}O) values in parts per thousand (‰) relative to the PDB standard. The standard deviation of replicate measurements is typically 0.1 ‰ and 0.2 ‰ for $\delta^{13}C$ and $\delta^{18}O$, respectively. Oxygen isotopes do provide ecological information (Kohn et al. 1996; Sponheimer and Lee-Thorp 1999c; Sponheimer and Lee-Thorp 2001), although they are much better known as paleoclimatic proxies (e.g., Prentice and Denton 1988; Ayliffe and Chivas 1990). For this reason, and because of space constraints, we will not discuss them as paleoecological indicators here.

The relationship between dietary $\delta^{13}C$ and enamel apatite $\delta^{13}C$ has been well-studied. Unlike collagen, apatite tends to reflect the $\delta^{13}C$ of the "whole" or "bulk" diet, and not just the protein component (Ambrose and Norr 1993; Tieszen and Fagre 1993). Thus, apatite and bone collagen $\delta^{13}C$ provide different perspectives on an individual's diet. Indeed, if one wanted to obtain the most complete picture of an individual's diet, one should analyze both collagen and apatite, although this rarely happens in practice. Most important for our purposes here, however, is that enamel apatite provides a good average dietary signal and will equally reflect the consumption of vegetable and animal foods. Interestingly, however, it is evident that the relationship between dietary $\delta^{13}C$ and apatite $\delta^{13}C$ is not constant. Rodent apatite tends to be enriched by about +10 ‰ compared to diet (Ambrose and Norr 1993; Tieszen and Fagre 1993), while large mammal apatite is enriched by about +13 ‰ (Lee-Thorp et al. 1989b; Cerling and Harris 1999; Passey et al. 2005). These differences must be borne in mind when comparing rodent and non-rodent $\delta^{13}C$ but are of little significance for the present discussion.

The South African Australopiths and Early *Homo*

As in the initial bone collagen study by Vogel and van der Merwe (1977), the South African australopith studies were based upon the distinct isotopic signatures of C_3 (trees, bushes, shrubs, and forbs) and C_4 plants (tropical grasses and some sedges). In the early 1990s, it was generally believed that *Australopithecus africanus* had a diet that of fleshy fruits and leaves, much like the modern chimpanzee (*Pan troglodytes*), while *Paranthropus robustus* consumed smaller, harder foods such as nuts (Grine 1981, 1986; Grine and Kay 1988; Ungar and Grine 1991). As these are all C_3 foods, one would then expect that *Australopithecus* and *Paranthropus* would have $\delta^{13}C$ values indistinguishable from those of C_3 browsers and frugivores. Several studies have shown, however, that the $\delta^{13}C$ of both australopiths is very distinct from that of their C_3-consuming coevals (Lee-Thorp et al. 1994, 2000; Sponheimer and Lee-Thorp 1999a; van der Merwe et al. 2003; Sponheimer et al. 2005a).

Figure 3 shows the combined australopith dataset from Makapansgat, Sterkfontein, Kromdraai, and Swartkrans. Analysis of variance and Fisher's PLSD test show that both *Australopithecus* ($x = -7.1$ ‰, s.d. = 1.8, $n = 19$) and *Paranthropus* ($x = -7.6$ ‰, s.d. = 1.1, $n = 18$) are strongly different from contemporaneous C_3 ($x = -11.5$ ‰, s.d. = 1.3, $n = 61$) and C_4 consumers ($x = -0.6$ ‰, s.d. = 1.8, $n = 60$) ($P < 0.0001$), but cannot be distinguished from each other. This distinction between the hominins and other fauna cannot be ascribed to diagenesis, as there is no evidence that browser or grazer $\delta^{13}C$ has been altered, and diagenesis should affect hominins and non-hominin fauna alike. If we take the mean $\delta^{13}C$ of C_4- and C_3-consuming herbivores as indicative of pure C_4 and C_3 diets, respectively, this would indicate diets of about 35–40 % C_4 vegetation for both *Australopithecus* and *Paranthropus*. Thus, both were eating considerable quantities of C_4 resources, possibly grasses, sedges, or animals that ate these plants. None of these possibilities were expected, as extant apes are not known to consume these foods to a significant degree (see chapter "▶ Great Ape Social Systems," Vol. 2; Goodall 1986; McGrew et al. 1982). Indeed, even in environments where C_4 foods are readily available, chimpanzee $\delta^{13}C$ does not indicate any C_4 consumption

(Schoeninger et al. 1999; Carter 2001). This suggests a fundamental niche difference between the australopiths and extant apes, which is not so surprising given the vast differences in their craniodental morphology (Grine 1981; Kay 1985; Teaford et al. 2002; Ungar 2004).

It is worth noting that the evidence of extensive C_4 consumption was not the only surprise in the australopith dataset. Indeed, hominin $\delta^{13}C$ turned out to be more variable than virtually all modern and fossil taxa that have been analyzed in South Africa (Lee-Thorp et al. 1994, 2000; Sponheimer et al. 1999, 2001, 2003b; Codron 2003; van der Merwe et al. 2003). There is considerable evidence that South African australopith habitats became more open between ~3.0 Ma and ~1.7 Ma (Vrba 1980, 1985; Reed 1997; Luyt and Lee-Thorp 2003), and it might be argued that this environmental change forced the australopiths to modify their diets over time, leading to their unusually variable $\delta^{13}C$. Yet, linear regression demonstrates that there is no relationship between hominin $\delta^{13}C$ and time ($P = 0.63$, $R^2 = 0.01$; Fig. 4) and there are no significant differences in hominin $\delta^{13}C$ between 3.0 Ma Makapansgat Member 3, 2.5 Ma Sterkfontein Member 4, and 1.8 Ma Swartkrans Member 1 (ANOVA, $P = 0.14$). Indeed, what is most striking about these data is the lack of change in hominin $\delta^{13}C$ in the face of pronounced environmental change. Somewhat paradoxically, however, within any given time period (Member), hominin $\delta^{13}C$ is highly variable. This might simply indicate that the australopiths were extremely opportunistic primates with wide habitat tolerances that always inhabited a similarly wide range of microhabitats. This would be consistent with Wood and Strait's (2004) recent suggestion that early hominins were eurytopic rather than ecological specialists.

In the case of *A. africanus*, the variability is so great that one might be excused for asking if there are not two ecologically distinct taxa presently commingled within its hypodigm (see chapters "▶ Analyzing Hominin Phylogeny: Cladistic Approach" and "▶ The Species and Diversity of Australopiths," Vol. 3). In fact, if one includes the numbers for the three teeth (STW 236, STW 213i, STW 207) that are possibly, but not definitively, attributed to *A. africanus* (van der Merwe et al. 2003), then this taxon would range from nearly pure C_3 to nearly pure C_4

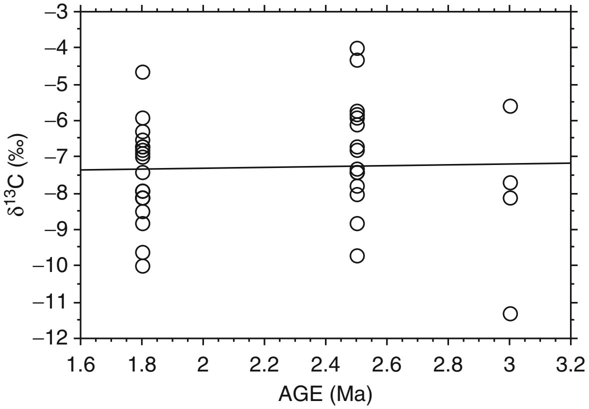


Fig. 4 $\delta^{13}C$ of South African hominins through time. No temporal trend is evident, despite abundant evidence that South African hominin environments changed during this time

diets. Stated otherwise, the range of $\delta^{13}C$ within *A. africanus* (−1.8 to −11.3 ‰) would be nearly as great as the entire range for ecologically disparate *Papio* and *Theropithecus* combined (+0.4 to −12.6 ‰) (Lee-Thorp et al. 1989). In and of themselves, stable isotopes cannot address the question of *A. africanus* unity; but numerous researchers have suggested that *A. africanus* might demonstrate more morphological variability than would be expected for a single taxon (Kimbel and White 1988; Clarke 1994; Lockwood 1997; Moggi-Cecchi et al. 1998). Hence, the possibility of two taxa, one subsisting largely on C_4 foods and the other on C_3 foods, cannot be dismissed. Further work addressing this hypothesis is warranted, but for the time being, we continue to work under the assumption that the specimens currently assigned to *A. africanus* represent a single species.

In short, both South African australopiths consumed about 35–40 % C_4 vegetation and have highly variable carbon isotope compositions. But how does this compare with early *Homo*? Lee-Thorp et al. (2000) tested for isotopic differences between *Paranthropus* and rarer early *Homo* specimens from Member 1 at Swartkrans. They assumed that if *Homo* consumed more animal foods, as was widely held, then its $\delta^{13}C$ values should be enriched compared to the australopiths because many savanna animals eat C_4 grasses. Surprisingly, though, *Homo* $\delta^{13}C$ was very similar to that of the australopiths, and the results must be interpreted in a similar way: roughly 25 % early *Homo*'s diet came from C_4 sources that included C_4 grasses, C_4 sedges, C_4 animal products, or some combination of these foods (see chapters "▶ The Earliest Putative *Homo* Fossils" and "▶ Defining the Genus *Homo*," Vol. 3; Lee-Thorp et al. 2000). However, only three *Homo* specimens from one site have been analyzed and published, and thus comparisons with the more numerous australopith data must be viewed with caution.

What C_4 Foods?

Which C_4 foods did the South African australopiths utilize? This question is quite significant, as the use of these different resources might have a variety of physiological, social, and behavioral implications. For instance, if australopiths had a grass-based diet similar to the modern gelada baboon (*Theropithecus gelada*), this would almost certainly indicate that their diets were less nutrient dense than those of modern apes, possibly placing important limitations on burgeoning hominin brains and sociality (Aiello and Wheeler 1995; Milton 1999). The converse that australopiths ate diets rich in animal foods would indicate a leap in dietary quality over modern apes. This could have been a crucial step toward hominin encephalization, the development of stone tool industries, and increased social complexity (Milton 1999). Similarly, it has been suggested that consuming the underground storage organs of plants like C_4 sedges would represent an increase in dietary quality over that of extant great apes because they are lower in dietary fiber than ape fallback foods (Conklin-Brittain et al. 2002). We will now discuss the evidence for the consumption of C_4 grasses, C_4 sedges, and animal foods in turn.

The Case for Grasses

Some researchers noted that the robust craniodental anatomy of the australopiths might have been an adaptation for eating grass seeds and roots as do modern gelada baboons (*Theropithecus gelada*) (Jolly 1970; Wolpoff 1973). A dental microwear study of modern geladas showed that their molar microwear is dominated by scratches with little evidence of pitting (Teaford 1992), however, which is quite unlike the heavily pitted molars of the australopiths (Grine 1986; Grine and Kay 1988). This result is hardly surprising, though, as it would seem unlikely that relatively large-brained hominins could be sustained on gelada-like diet (high in fiber, low in protein and long-chain polyunsaturated fatty acids) without supplementation with higher-quality foods. Furthermore, the stable isotope results do not indicate a pure C_4 diet, but rather one in which C_4 foods are very important, but not exclusive. Therefore, even if the C_4 component did originate from grasses, one would not expect australopiths to have *Theropithecus*-like microwear.

One might expect, however, that australopiths and savanna baboon populations that consume large quantities of grass seasonally would show similarities in dental microwear (Altmann and Altman 1970; Harding 1976; Dunbar 1983; Strum 1987), and indeed two recent studies of *Papio* molar microwear noted a more australopith-like frequency of pitting than was found in *Theropithecus* (Daegling and Grine 1999; Nystrom et al. 2004). In addition, a recent elemental analysis of australopith tooth enamel showed that while *Australopithecus*, and to a lesser extent *Paranthropus*, had higher Sr/Ca ratios than carnivores, browsers, and papionins, their Sr/Ca was quite similar to grazers. In fact, the unusual combination of high Sr/Ca and low Ba/Ca in *Australopithecus* has only been found in modern fauna that heavily utilize the underground portions of grasses such as warthogs (*Phacochoerus africanus*) and African mole rats (*Cryptomys hottentotus*) (Sponheimer et al. 2005b). These elemental data are still preliminary and certainly cannot be used to state affirmatively that early hominins consumed grasses. Nevertheless, they are entirely consistent with the possibility and suggest avenues for future research.

The Case for Sedges

Sedges have also received attention as a potential C_4 food for australopiths. Conklin-Brittain et al. (2002) argued that a trend toward desiccation in the Pliocene eroded forests and ultimately forced australopiths into new, more open habitats (see chapters "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3, "▶ Zoo geography: Primate and Early Hominin Distribution and Migration Patterns," Vol. 1, and "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition," Vol. 2). Although the degree, manner, and timing of this deterioration are a matter of some debate, the fact that it occurred is not (Vrba 1985; DeMenocal 1995; Feibel 1997). Conklin-Brittain et al. (2002) reasoned that this loss of forest habitat forced australopiths into environments that were most similar to their ancestral forest homes, namely, wetlands, swamps, and river margins. Sedges are readily available in these environments and have been argued to be among the possible sources of the C_4 signal in australopiths (Sponheimer and Lee-Thorp 1999a; Conklin-Brittain et al. 2002). Some sedges have underground storage organs that have protein levels equal to those of most chimpanzee foods (9 % crude protein), but much lower fiber levels (16 % fiber) than foods consumed by chimpanzees (33 %) (Conklin-Brittain et al. 2002). Thus, the regular inclusion of sedges in australopith diets might represent an increase in dietary quality over extant great apes. Equally important, the underground portions of sedges would be relatively inaccessible to most mammals, yet readily accessible to hominins with crude-digging implements (Hatley and Kappelman 1980), making sedges a high-quality resource for which there is very little competition. Such foods might have been particularly important during the dry season when other preferred dietary resources were scarce. Moreover, there is evidence of humans and other primates consuming sedges. Modern humans have consumed sedges like *Cyperus esculentus* and *C. papyrus* for thousands of years (Tackholm and Drar 1973; Defelice 2002). Western lowland gorillas (*Gorilla gorilla gorilla*) have also been observed consuming the pith of sedges, although in small quantities (see chapter "▶ Great Ape Social Systems," Vol. 2; Doran and McNeilage 1998). Finally, *Australopithecus*' high Sr/Ca is consistent with the consumption of sedge USOs (Sillen et al. 1995; Sponheimer et al. 2005b), although as previously mentioned this is also consistent with the consumption of grass USOs.

But how likely is it that the observed C_4 signal in early hominins was derived from C_4 sedges? Although 33 % of the world's sedges use the C_4 photosynthetic pathway (Sage et al. 1999), it is incorrect to assume that all or even most sedges available to australopiths would have utilized the C_4 pathway. Although 65 % of Kenyan sedges reportedly use C_4 photosynthesis (Hesla et al. 1982), only 35 % do in South Africa (Stock et al. 2004). More to the point, a study of sedges in riverine habitats similar to those inhabited by australopiths found that only 28 % use C_4 photosynthesis (Sponheimer et al. 2005a). Thus, unless the South African australopiths deliberately sought out C_4 sedges or the distribution of sedges was markedly different during the Pliocene, the australopiths would have had to have had a diet of 100 % sedges to come close to producing the observed 35–40 % C_4 signal. A slightly more probable scenario than this extreme sedge specialization is that the australopiths deliberately sought out C_4 sedges with particularly well-developed rootstocks such as *Cyperus papyrus*, and thus a diet of 35–40 % sedges would have been sufficient to explain the australopith carbon isotope values. Yet, this too is unlikely, for although these highly edible sedges are common in extensive perennial wetlands like the Okavango Delta, they are rare in the woodland/bushland habitats that were inhabited by australopiths (Reed 1997; Peters and Vogel 2005).

All told, the available data suggest that even if sedges did constitute an important resource for early hominins, they were likely supplemented with other C_4 foods. Alternatively, if other C_4 foods were not consumed, australopiths would have had to have been true sedge specialists to account for the strong C_4 signatures observed in most specimens. It is worth noting, however, that some early hominin habitats in East Africa such as the wetlands of the Eastern Lacustrine Plain at Olduvai Gorge (Hay 1976; Deocampo et al. 2002) might have been better sources of edible C_4 sedges, and Puech et al. (1986) have also suggested that the dental microwear of early East African hominins is consistent with the consumption of such foods (see below for isotopic analysis of eastern African hominins).

The Case for Animal Foods

Animal foods can mean many different things including large and small vertebrates, invertebrates, and even bird's eggs. These foods can also be acquired in a variety of ways including active hunting of large games, passive scavenging, and gathering of insects and eggs (see chapters "▶ The Hunting Behavior and Carnivory of Wild Chimpanzees" and "▶ Cooperation, Coalition, Alliances," Vol. 2). Although chimpanzees are known to hunt a variety of small vertebrates such as red colobus monkeys (*Piliocolobus badius*) and blue duiker (*Cephalophus monticola*), these are pure C_3 consumers (Teleki 1981; Goodall 1986). Therefore, intake of these foods could not contribute to the C_4 component of australopith diets. More likely sources of the reported C_4 signal include small grass-eating taxa such as hyraxes (*Procavia* spp.) and cane rats (*Thryonomys swinderianus*). The young of larger species would also be tempting targets. For instance, the young of antelope like reedbuck (*Redunca arundinum*) lies hidden and largely helpless for the first several months of life, making them an easy prey for enterprising hominins.

Arthropods are also potential C_4 foods. Baboons are known to eat grass-eating grasshoppers (Acrididae) almost exclusively during temporary gluts (Hamilton 1987). Grass-eating termites represent another intriguing possibility, particularly given recent studies suggesting that bone tools from Swartkrans were used to extract termites from mounds (Backwell and D'Errico 2001). Stable isotope studies of termites in African savanna environments have shown that they could have contributed to the australopiths' ^{13}C-enrichment (Boutton et al. 1983; Sponheimer et al. 2005a). While termites range from nearly pure C_3 to pure C_4 consumers, the vast majority of savanna termites, even in densely wooded riverine microhabitats, consume significant proportions of C_4 foods. In fact, termites throughout Kruger National Park eat 35 % C_4 vegetation on average (Sponheimer et al. 2005a; Fig. 5). Thus, termite consumption by australopiths in woodland savanna and even in riverine forest would be expected to impart some C_4 carbon to consumers. On the other hand, the fact that so few termites have a pure C_4 signal makes it unlikely that termite consumption alone was the source of the strong C_4 signal of australopiths, because it would require a diet of nearly 100 % termites.

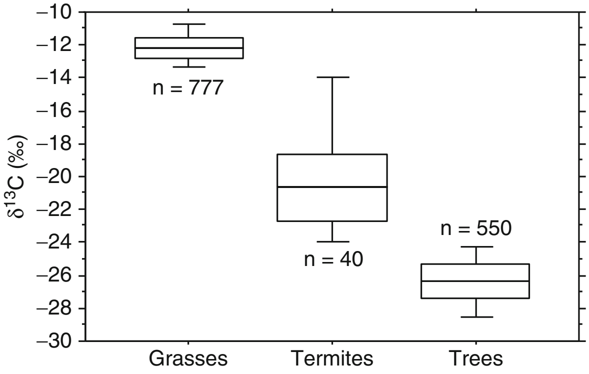


Fig. 5 δ^{13}C for termites, trees, and grasses in Kruger National Park. The boxes represent the 25th–75th percentiles (with the medians as a *horizontal line*) and the whiskers show the 10th–90th percentiles. Note that while termites have highly variable carbon isotope compositions, the vast majority of specimens have mixed C_3/C_4 signatures

Alternatively, if the hominins selectively preyed upon grass-specialist harvester termites (*Trinervitermes*, *Hodotermes*) with virtually pure C_4 diets, a diet of about 35–40 % termites would be sufficient to produce the observed hominin carbon isotope ratios. This scenario, however, is highly unlikely because these C_4 termites are much less common than those with mixed C_3/C_4 diets in woodlands today; and while harvester termites are more abundant in open grasslands and during acute droughts (Braack and Kryger 2003), there is no reason to believe that australopiths frequented such open environments or that drought conditions were so preponderant (see chapters "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3 and "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1). Moreover, while *Trinervitermes* builds highly visible aboveground nests (mounds), *Hodotermes* does not, making it much less conspicuous on the landscape (Carruthers 1997; Stuart and Stuart 2000). Thus, it is possible and even likely that termites contributed in some way to the unusual $\delta^{13}C$ values of australopiths, but other C_4 resources were almost certainly consumed in considerable quantities.

It has been suggested that hominid dental anatomy was not well suited for the processing of animal foods (Teaford et al. 2002), but this observation only pertains to a limited class of animal foods. A great many animal foods require little, if any, oral processing. Termites, grasshoppers, ants, grubs, eggs, and a variety of other insect delicacies may be consumed whole, and even small vertebrates can be swallowed whole or in a few pieces (Smithers 1983). Brains, marrow, and other soft tissues can also be consumed without oral processing. In addition, no experiments have been conducted to investigate the actual oral and/or preoral processing necessary to consume the muscle tissue of small vertebrates. Thus, it seems unwise to unduly limit the potential foods for australopiths until such studies have been undertaken. Furthermore, the consumption of animal foods is common among mammals without seemingly appropriate dentition. One obvious example is the aardwolf (*Proteles cristatus*) which consumes hundreds of thousands of termites per night with largely nonfunctional, obsolescent dentition (Smithers 1983). In some cases, this apparent disjunction between dental morphology and trophic behavior might result from the dentition being adapted for others, more mechanically challenging foods in an animal's diet. For example, capuchin monkeys (*Cebus apella*) have large, bunodont dentition with thick enamel adapted for consuming fruits and hard nuts. Nonetheless, up to 50 % of capuchin diets can come from animal foods, although the average is closer to 25 % (Fleagle 1999; Rosenberger and Kinzey 1976; Rosenberger 1992). Similarly, Ungar (2004) has argued that among hominoids, differences in dental morphology primarily reflect their multifarious fallback foods, rather than their preferred foods during times of plenty.

What Does It Mean?

All told, we still cannot be certain which C_4 resources were utilized by South African australopiths. Grass roots, grasshoppers, bird's eggs, lizards, rodents, and young antelopes might have been important C_4 resources, particularly during the dry season when little other food was readily available. Succulent plants like euphorbias (Euphorbiaceae) and aloes (Aloaceae) (which are rare in most woodlands but have $\delta^{13}C$ values that are sometimes indistinguishable from those of C_4 grasses) are also possibilities; for although they are often poisonous to humans (and presumably chimpanzees), they are occasionally utilized by baboons and humans (Codron 2003; Peters and Vogel 2005). Further work on dental microwear and morphology, elemental analysis, and the potential availability and nutritional properties of foods may make it possible to identify these C_4 resources with greater confidence. At present, however, it seems likely that australopiths utilized a wide variety of these foods.

Despite this uncertainty, we should not lose sight of the most significant aspect of these stable isotope data, namely, that australopiths increased their dietary breadth compared to extant apes by consuming novel C_4 resources, *regardless* of what these resources were (see chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). Similar evidence for increased dietary breadth is also evident in their thicker enamel, larger postcanine dentition, and greater mandibular corpus robusticity, all of which point to the consumption of hard objects beyond the capabilities of extant apes (Teaford et al. 2002). Thus, the fundamental trophic difference between australopiths and extant apes might be that when confronted with increasingly open areas, apes continue to exploit the foods that are most abundant in forest environments (McGrew et al. 1982), whereas australopiths utilized novel C_4 resources in addition to forest foods. There would have been a number of advantages to such a dietary strategy. It would have allowed australopiths to survive and even thrive in a much greater variety of habitats than do modern great apes, potentially allowing expansion of their range. Similarly, the increased dietary breadth could have buffered australopiths against climatic change and habitat loss. Another implication of increased dietary flexibility might be decreased foraging time and mobility, allowing for increased social interaction and possibly greater social complexity. This flexibility could also have increased dietary quality over that of extant apes by adding low-fiber underground storage organs and protein- and lipid-rich animal foods to australopith menus. This might have been an important step leading to greater encephalization and development of the genus *Homo* (see chapter "▶ Evolution of the Primate Brain," Vol. 2; Aiello and Wheeler 1995; Milton 1999; Conklin-Brittain et al. 2002).

If increased dietary breadth was a fundamental australopith adaptation, what are we to make of the later robust australopiths in which the dental adaptations reached their most specialized form? They are believed to have been specialist hard object feeders that were eventually replaced by our *Homo* forebears who, for the first time, had regular access to higher quality animal foods (Aiello and Wheeler 1995; Milton 1999). An alternative explanation, however, is that the robust australopithecines were the quintessence of the trend towards dietary diversity because they could access the foods of their progenitors as well as harder foods. One might then argue that they were supplanted by *Homo* not because they ate different kinds of foods, but because *Homo* was more efficient at procuring these resources due to increased use of extra-oral processing (e.g., stone tools) and greater planning depth. It is believed, for instance, that early *Homo* increased access to bone marrow from scavenged or hunted carcasses of medium to large mammals by using stone tools (e.g., Blumenschine 1987), whereas there is a debate as to whether or not robust australopiths utilized such technology (e.g., Leakey et al. 1964; Susman 1988; Semaw et al. 1997; de Heinzelin et al. 1999). Furthermore, where australopiths may have eaten antelope lambs only when they stumbled upon them, *Homo* may have had superior planning depth and followed female antelopes back to their young, capturing them only when the mother left once more.

New Data from Beyond South Africa

For nearly 15 years, carbon isotope analysis had only been undertaken on South African early hominins, but now studies have been completed on both central and eastern African hominin specimens (van der Merwe et al. 2008; White et al. 2009; Cerling et al. 2011, 2013; Lee-Thorp et al. 2012; Wynn et al. 2013; Fig. 6). These new data have dramatically increased our understanding of the taxonomic, regional, and temporal dimensions of early hominin diet (data available at http://dx.doi.org/10.6084/m9.figshare.710649; Sponheimer et al. 2013).

For instance, it now appears that before 4 Ma, eastern African hominins had carbon isotope compositions indicating primarily C_3 consumption (White et al. 2009; Cerling et al. 2013). It also appears that by about 3.5 Ma, C_4 food consumption became significant, if highly varied, within eastern African taxa such as *A. afarensis* and *Kenyanthropus platyops* (Cerling et al. 2013; Wynn et al. 2013).

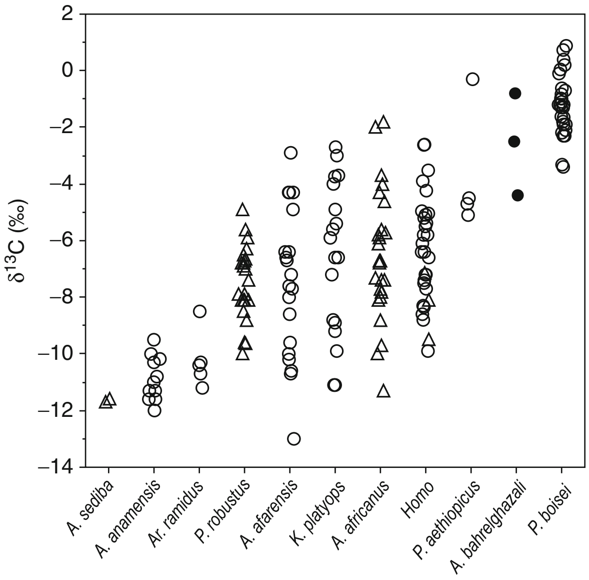
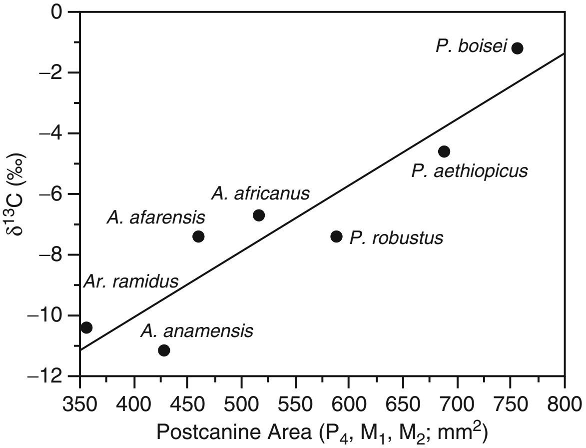


Fig. 6 Early hominin taxa from southern Africa (*open triangles*), eastern Africa (*open circles*), and central Africa (*closed circles*) arranged from lowest to highest $\delta^{13}C$ values

Fig. 7 Linear regression showing that australopith postcanine area predicts $\delta^{13}C$ values ($r^2 = 0.86$, $t(5) = 5.50$, $P < 0.01$). The relationship between $\delta^{13}C$ values and mandibular cross-sectional area at M1 is not shown (see Sponheimer et al. 2013)



There is also strong evidence for regional differences. Most notably, *P. robustus* in southern Africa and *P. boisei* in eastern Africa, despite their marked morphological similarities, have highly different $d^{13}C$ values ($P < 0.001$), suggesting that the latter had a diet dominated by C_4 (or less likely CAM) vegetation (van der Merwe et al. 2008; Cerling et al. 2011). Concomitantly, there is now strong isotopic evidence of niche differentiation between *Homo* and *Paranthropus* in eastern Africa, which contrasts with the broadly similar $\delta^{13}C$ values of these genera in southern Africa (Lee-Thorp et al. 2000). Preliminary observations also suggest a relationship between masticatory morphology and australopith carbon isotope compositions, with postcanine tooth size and mandibular cross-sectional area at M_1 both increasing as do $\delta^{13}C$ values (Sponheimer et al. 2013; Fig. 7). This could indicate that C_4 food consumption was among the driving forces behind the trend toward masticatory robusticity within the australopiths.

Given this, it is surprising that evidence for environmentally driven changes in australopiths $\delta^{13}C$ values remains equivocal. The transition to significant C_4 consumption at about 3.5 Ma is not obviously related to increased availability of C_4 grass (Sponheimer et al. 2013), and changes in the habitat of *A. afarensis* are not clearly reflected in its $\delta^{13}C$ values (Wynn et al. 2013). It remains possible that an environmental signal has become obscured by the poor temporal and environmental resolution of the existing hominin fossil record and that climatic/environmental change at precessional or shorter time scales did drive hominin $\delta^{13}C$ values (Hopley and Maslin 2010), but this cannot be tested at present. We note, however, that even if changes in the abundance of C_4 grass did not influence hominin $\delta^{13}C$ values, it remains possible that other environmental parameters such as tree or mammalian diversity did (Sponheimer et al. 2013).

As to what C_4 resources hominins post 4 Ma ate, it should be remembered that "early hominin diet" or even "australopith diet" is chimerical given that the available carbon isotope data now span more than three million years, 11 species, and major differences in masticatory anatomy and associated archaeology (see chapters "▶ Analyzing Hominin Phylogeny: Cladistic Approach" and

"▶ The Species and Diversity of Australopiths," Vol. 3; Sponheimer et al. 2013). Given this, and the likely corollary of marked diversity of early hominin diets, it is not only plausible but probable that C_4 food acquisition and consumption differed among hominin species within a broad region like eastern Africa. For instance, given *Paranthropus boisei*'s high $\delta^{13}C$ values, thick, robust mandibles, low-cusped cheek teeth, and diminutive incisors and canines, it is improbable that its major C_4 dietary input was meat. Even savanna carnivores may not attain such high $\delta^{13}C$ values (Codron et al. 2007). It is, therefore, most parsimonious to ascribe the preponderance of its C_4 "signal" to the direct consumption of C_4 plant foods like grasses or sedges. As to what parts of these plants were consumed, given the discussion earlier in this manuscript, we are a long way from knowing. The situation for contemporaneous *Homo* might be different, though. Its dental morphology (Ungar 2004), the general belief that it produced (rather than *Paranthropus*), the majority of its associated archaeological record (Leakey et al. 1964), and arguments derived from energetics (Aiello and Wheeler 1995) are consistent with *Homo* having consumed greater amounts of animal protein from which it might have derived its C_4 carbon.

Conclusion

Stable isotope studies have made an important contribution to our understanding of early hominin diets. In the case of Neanderthals, stable isotopes strongly support the contention that they were highly carnivorous, primary predators. As for the australopiths, stable isotopes suggest that they broadened the ancestral ape resource base to include C_4 foods, which coupled with bipedalism, and allowed them to pioneer increasingly open and seasonal environments. Yet, as is the case with all paleodietary techniques, stable isotopes leave a great many important questions unresolved. Particularly important are the equifinality problems that are common in stable isotope studies. In other words, many different diets can lead to the same stable isotope signature. For instance, carbon isotopes often cannot distinguish between diets as different as folivory, frugivory, and carnivory. And although some progress has been made using oxygen isotopes to break such equifinalities (Sponheimer and Lee-Thorp 1999c; Carter 2001), there is little reason to believe that this problem can be circumvented entirely by relying on stable isotopes. In the end, stable isotopes are one tool among many, all of which provide a slightly different window into the diets of our ancestors. Thus, where stable isotopes cannot determine the favored prey of Neanderthals, faunal analysis has much to contribute (Speth and Tchernov 2001), and when carbon isotopes remain silent on the topic of australopith fallback foods, dental morphology may jump into the fray (Ungar 2004). Thus, stable isotopes will prove most informative when pursued as part of a larger, integrated paleodietary investigation.

That being said, stable isotopes themselves still have a great deal to tell us about the diets of our ancestors. To date, only Pliocene and early Pleistocene African hominins, Neanderthals, and AMH have been analyzed for stable isotopes to any significant extent, leaving the entire continents and large periods of time virtually unexplored. Future stable isotope studies will surely bridge these gaps, and in so doing greatly increase our knowledge of early hominin diets. Yet, we should not be satisfied to merely work our way through previously neglected or unattainable material, but should seek to push the limits of the technique itself. Improving our knowledge of the stable isotope compositions of modern plants and mammals, investigating how physiology affects diet-tissue spacing, and refining organic extraction techniques so that nitrogen isotopes can be analyzed for a wider variety of taxa will not only improve our ability to reconstruct paleodiets but will also enable us to address questions in ways that were previously unimaginable. Hopefully, such actualistic and experimental work will serve to hone this already exciting paleodietary tool.

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Estimation of Basic Life History Data of Fossil Hominoids

Helmut Hemmer

Contents

Abstract

Relationships between the life cycle and body mass, brain mass, and relative brain size of extant primates can be used to estimate life history parameters of extinct species. Methods to predict these key variables from available cranial and postcranial materials of fossil hominoids, especially hominids, are compiled and evaluated. The use of different concepts of scaling relative brain size is discussed. Brain mass and constant of cephalization data were used as the source material for the estimation of the age at eruption of the first lower molar, the age at female sexual maturity, the age at first breeding, and the maximum life span. Such data support the interpretation of the Late Miocene *Sahelanthropus tchadensis* as a taxon possibly related to the hominid stem species near the splitting of chimpanzee and hominid lines; confirm the fundamental nature of the australopithecines as progressive apes, not as humans; and support the view of a close relationship of the Early Pleistocene *Homo* paleopopulation of Dmanisi (Georgia) to the earliest Pleistocene African *Homo* populations.

H. Hemmer (✉)
Institut für Zoologie, Johannes Gutenberg-Universität Mainz, Mainz, Germany
e-mail: h.hemmer-mainz@gmx.de

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Introduction

Fossil bones are the material of classic osteological studies as a base of systematic and phylogenetic conclusions as well as the understanding of functional correlations of morphological structures. They also bear information that may be used for a two-step computing procedure to estimate fundamental life history and ecological and behavioral data that open a progressive level of insight into ecological relations.

Life history study is understood as an approach in evolutionary biology, identifying ontogenetic variables and then asking what impact those variables have on population size and composition. Relationships between the life cycle and anatomical variables, such as body size and brain size, are of particular interest because they can be used to estimate life history parameters of extinct species (Hemmer 1974, 2003; Gingerich et al. 1982; De Rousseau 1990; Harvey 1990; Smith and Tompkins 1995), even if there are also life history components independent of brain and body size (Harvey and Read 1988).

The first step of such life history data calculation is the estimation of body mass as a key variable, supported by the estimation of brain mass, from available fossil remains. The second step then takes advantage of the first-level results to look for estimates of parameters of the individual's life cycle, such as the age at first reproduction or the maximum life span. How this subsequently affects higher levels of organization as, e.g., ecological aspects or population growth and evolution, is an additional step of life history consideration (De Rousseau 1990; Hemmer 2003; Kappeler et al. 2003). This chapter focuses on the way to evaluate such basic information concealed in fossil bones, to look for hominoid, especially hominid, life history aspects. It does not deal with life history correlates as left by the processes of growth, with "osteobiographic" techniques (Boyde 1990; Bromage 1990).

Life History Correlations

Basic primate life history dimensions were found to correlate with body mass (Harvey and Clutton-Brock 1985; Harvey et al. 1987; Lee and Kappeler 2003; Table 1), with absolute brain size (Sacher 1975; Harvey et al. 1987; Smith 1989; Smith et al. 1995; Deaner et al. 2003), and with relative brain size (Hemmer 1974). Brain size is more closely correlated with several life history variables, such as the age at sexual maturity or at first breeding, than is body size (Harvey et al. 1987). Unfortunately, data compilation in landmark publications (Harvey and Clutton-Brock 1985; Harvey et al. 1987) was confounded by conversion of cranial capacity with brain mass using a relationship 1 $cm^3 = 1$ g (Smith et al. 1995). Other studies were based on either cranial capacity or brain mass (Sacher 1975; Smith et al. 1995; Table 2). The factor related to brain size was considered to be maturation rate as a whole rather than any one of its aspects (Smith 1989). There is an extremely high correlation of the age at eruption of the first lower molar, as a rather stable marker of growth with relatively low variance, and brain size ($r = 0.98$). When the effect of

Table 1 Relationships between life history variables (days) and adult female body mass (FBM, g) in primates

Life history variable	*r*	Equation
Gestation length (GL)	0.74	$\log GL = 0.13 \log FBM + 1.775$
Weaning age (WA)	0.91	$\log WA = 0.56 \log FBM + 0.433$
Age at maturity, female (AMF)	0.89	$\log AMF = 0.51 \log FBM + 1.253$
Age at maturity, male (AMM)	0.89	$\log AMM = 0.47 \log FBM + 1.471$
Age at first breeding, female (AFB)	0.92	$\log AFB = 0.44 \log FBM + 1.638$
Interbirth interval (IBI)	0.86	$\log IBI = 0.37 \log FBM + 1.464$
Life span (LS)	0.78	$\log LS = 0.29 \log FBM + 2.893\ 1$

Harvey and Clutton-Brock (1985, Tables 4 and 5) or Harvey et al. (1987, Tables 16.3 and 16.4); correlation coefficients based not on the species but on the subfamily level

Table 2 Relationships between life history variables and brain size in anthropoid primates

Life history variable	*r*	Equation	Source and sample
M_1 eruption age (years) (M_1EA)	0.98	$\ln M_1EA = 0.582 \ln CrC - 2.405$	Smith et al. (1995): 14 anthropoid species
Life span (years) (LS)	0.835	$\log LS = 0.379 \log BrM + 0.640$	Sacher (1975): 43 anthropoid species

CC cranial capacity (cm^3), *BrM* brain mass (g)

body mass is held constant in multiple regression, the partial correlation of M_1 eruption and adult brain size remains $r = 0.90$ (Smith 1989).

The use of relative brain size (constant of cephalization; see later) instead of absolute brain mass or cranial capacity in life history correlations (Hemmer 1974) eliminates the influence of body size and allows for some further improvement of the correlation coefficient with most variables. Allometric formulas that may be used as predictor equations for the estimation of life history data in fossil hominoid primates were calculated for the present contribution based on brain mass (brain and body mass data, Bauchot and Stephan (1969); life history data, Harvey and Clutton-Brock (1985)) to avoid the former 1:1 confusion with cranial capacity data. The results for the relationship of body size, brain size, and coefficient of cephalization with the life history corner-stages age at sexual maturity, age at first reproduction, and maximum life span (data taken from the compilation of Harvey and Clutton-Brock (1985): Table 1), as well as age at first lower molar eruption and at completion of the dentition [data taken from Smith (1989), with modifications by Smith et al. (1995)], are listed in Tables 3 and 4 and illustrated in Figs. 1 and 2.

Estimating Body Mass

Body size cannot be measured directly being an abstract concept not a concrete parameter. Size may variously be recorded, e.g., as head-body length or height at the withers in quadruped mammals or as stature in hominids, but for general use

Table 3 New life history variable allometries in anthropoid primates

Life history variable	*r*	*n*	Equation	Reliability for prediction in hominid evolution
Age at sexual maturity, female (months) (ASMF)	0.815	23	$\log \mathrm{ASMF} = 0.341 \log \mathrm{BM} + 0.349$ (LSR)	103 %, useless
			$\log \mathrm{ASMF} = 0.418 \log \mathrm{BM} + 0.059$ (RMA)	68 %, useless
	0.878	23	$\log \mathrm{ASMF} = 0.482 \log \mathrm{BrM} + 0.697$ (LSR)	24 %, useless
			$\log \mathrm{ASMF} = 0.549 \log \mathrm{BrM} + 0.568$ (RMA)	3 %, useful
	0.889	23	$\log \mathrm{ASMF} = 0.693 \log \mathrm{CC} + 0.889$ (LSR)	2 %, useful
			$\log \mathrm{ASMF} = 0.776 \log \mathrm{CC} + 0.801$ (RMA)	15 %, less useful
Age at sexual maturity, male (months) (ASMM)	0.797	13	$\log \mathrm{ASMM} = 0.287 \log \mathrm{BM} + 0.686$ (LSR)	No observed value for *Homo sapiens*
			$\log \mathrm{ASMM} = 0.360 \log \mathrm{BM} + 0.411$ (RMA)	
	0.857	13	$\log \mathrm{ASMM} = 0.440 \log \mathrm{BrM} + 0.919$ (LSR)	
			$\log \mathrm{ASMM} = 0.514 \log \mathrm{BrM} + 0.777$ (RMA)	
	0.878	13	$\log \mathrm{ASMM} = 0.664 \log \mathrm{CC} + 1.062$ (LSR)	
			$\log \mathrm{ASMM} = 0.756 \log \mathrm{CC} + 0.965$ (RMA)	
Age at first breeding, female (months) (AFB)	0.856	27	$\log \mathrm{AFB} = 0.315 \log \mathrm{BM} + 0.584$ (LSR)	84 %, useless
			$\log \mathrm{AFB} = 0.368 \log \mathrm{BM} + 0.385$ (RMA)	62 %, useless
	0.898	27	$\log \mathrm{AFB} = 0.445 \log \mathrm{BrM} + 0.913$ (LSR)	15 %, less useful
			$\log \mathrm{AFB} = 0.495 \log \mathrm{BrM} + 0.816$ (RMA)	<1 %, very useful
	0.902	27	$\log \mathrm{AFB} = 0.636 \log \mathrm{CC} + 1.096$ (LSR)	3 %, useful
			$\log \mathrm{AFB} = 0.704 \log \mathrm{CC} + 1.023$ (RMA)	16 %, less useful
Life span (years) (LS)	0.797	30	$\log \mathrm{LS} = 0.227 \log \mathrm{BM} + 0.511$ (LSR)	74 %, useless
			$\log \mathrm{LS} = 0.285 \log \mathrm{BM} + 0.297$ (RMA)	50 %, useless
	0.843	30	$\log \mathrm{LS} = 0.322 \log \mathrm{BrM} + 0.747$ (LSR)	24 %, useless
			$\log \mathrm{LS} = 0.382 \log \mathrm{BrM} + 0.634$ (RMA)	4 %, useful
	0.851	30	$\log \mathrm{LS} = 0.461 \log \mathrm{CC} + 0.877$ (LSR)	9 %, still useful
			$\log \mathrm{LS} = 0.541 \log \mathrm{CC} + 0.794$ (RMA)	9 %, still useful

(*continued*)

Table 3 (continued)

Life history variable	*r*	*n*	Equation	Reliability for prediction in hominid evolution
Age at eruption of first lower molar (AME)	0.971	11	$\log \text{AME} = 0.492 \log \text{BM} - 1.773$ (LSR)	37 %, useless
			$\log \text{AME} = 0.507 \log \text{BM} - 1.826$ (RMA)	31 %, useless
	0.985	11	$\log \text{AME} = 0.589 \log \text{BrM} - 1.091$ (LSR)	4 %, useful
			$\log \text{AME} = 0.598 \log \text{BrM} - 1.108$ (RMA)	6 %, still useful
	0.981	11	$\log \text{AME} = 0.796 \log \text{CC} - 0.814$ (LSR)	13 %, less useful
			$\log \text{AME} = 0.812 \log \text{CC} - 0.831$ (RMA)	16 %, less useful
Age at complete dentition (ACD)	0.966	10	$\log \text{ACD} = 0.533 \log \text{BM} - 1.347$ (LSR)	21 %, useless
			$\log \text{ACD} = 0.551 \log \text{BM} - 1.416$ (RMA)	16 %, less useful
	0.974	10	$\log \text{ACD} = 0.629 \log \text{BrM} - 0.588$ (LSR)	16 %. less useful
			$\log \text{ACD} = 0.648 \log \text{BrM} - 0.624$ (RMA)	20 %, less useful
	0.964	10	$\log \text{ACD} = 0.848 \log \text{CC} - 0.286$ (LSR)	25 %, useless
			$\log \text{ACD} = 0.880 \log \text{CC} - 0.321$ (RMA)	30 %, useless

Reliability for prediction in hominid evolution defined on the basis of the prediction error (PE, %) of the estimation for *Homo sapiens*; PE = (observed − predicted)/predicted × 100: $\text{PE} \leq 1$ %, very useful; $\text{PE} > 1 \leq 5$ %, useful; $\text{PE} > 5 \leq 10$ %, still useful; $\text{PE} > 10 \leq 20$ %, less useful; $\text{PE} > 20$ %, useless. Data for BM and BrM based on Bauchot and Stephan (1969); for CC, Hemmer (1971); for ASMF, ASMM, AFB, and LS, Harvey and Clutton-Brock (1985); and for AME and ACD, Smith (1989), with modifications by Smith et al. (1995)

BM body mass, *BrM* brain mass, *CC* constant of cephalization, *LSR* least-squares regression, *RMA* reduced major axis

body mass undoubtedly is the most reliable measure and the size variable of choice (Gingerich et al. 1982; Jungers 1988; Ruff and Walker 1993; Aiello and Wood 1994; Hemmer 2004). Skeletal predictors may allow to estimate body mass on principle on the base of dentition (Table 5), skull (Table 6), and postcranial elements (Tables 7 and 8).

There exists no direct biomechanical relationship between tooth and cranial variables and body mass (Jungers 1988), but such dimensions nevertheless depend on a general factor of size. Dentition measurements may allow us to predict a genetically programmed frame of body size than the real size an individual reached during its ontogeny. Allometric relationships between tooth size and body mass

Table 4 New life history variable allometries in hominoid primates

Life history variable	*r*	*n*	Equation	Reliability for prediction in hominid evolution
Age at first breeding, female (months) (AFB)	0.837	5	log AFB = 0.268 log BrM + 1.450 (LSR)	Useless, no significant correlation
			log AFB = 0.320 log BrM + 1.314 (RMA)	Useless, no significant correlation
	0.938	5	log AFB = 0.380 log CC + 1.563 (LSR)	9 %, still useful
			log AFB = 0.405 log CC + 1.524 (RMA)	6 %, still useful
Life span (years) (LS)	0.913	5	log LS = 0.296 log BrM + 0.888 (LSR)	8 %, still useful
			log LS = 0.324 log BrM + 0.814 (RMA)	4 %, useful
	0.950	5	log LS = 0.389 log CC + 1.059 (LSR)	<1 %, very useful
			log LS = 0.410 log CC + 1.027 (RMA)	2 %, useful

have been used to reach the goal of body mass estimation in extinct nongeneralized primates (Gingerich et al. 1982; Martin 1990; see discussion in Jungers 1990). This approach depends on what evolutionary grade of primate species is used to predict body mass (Conroy 1987), and would be a hazardous venture insofar as hominid evolution is concerned, in view of considerable changes of the relative size of the masticatory apparatus (Wolpoff 1973; Jungers 1988). The introduction of taxon-specific conversion factors (prediction by tooth size related to prediction by cranial or postcranial dimensions) may help to overcome that problem (as used in felid body mass prediction by Hemmer (2001, 2004)). It must also always be taken in mind that dentition-based body mass estimates cannot present real individual life weights but merely provide some idea about a statistic mean to be awaited at a given linear predictor measure within a population in question.

Cranial dimensions should depend more closely than tooth dimensions on individual ontogenetic body size modeling. They allow us to predict some "normal mass" of an individual. Cranial dimensions prove in that generalized function in some cases to be nearly as good or even better mass predictors as are some of the best postcranial ones (Aiello and Wood 1994; Kappelman 1996). Nevertheless, cranial dimensions may also considerably mislead on the other hand. Comparing the average body mass estimated at the base of seven cranial predictors to the actual body mass of the respective species, the average prediction error (PE) was found to be ±32.3 %, ranging from 0.5 % to 79.3 % (Martin 1990).

In limb bones, the genetic influences are supplemented by loading-related stimuli to a higher extant. They give evidence of an individual's muscular strength and

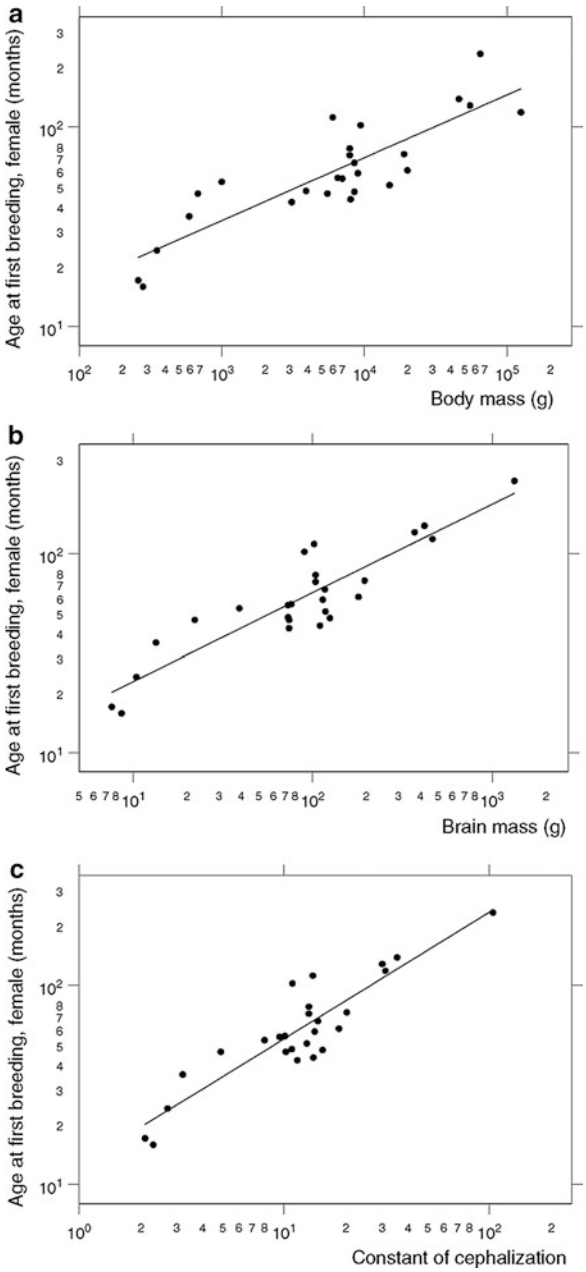


Fig. 1 Bivariate log–log plots (*lines*: least-squares regressions) of female age at first breeding (Data by Harvey and Clutton-Brock (1985), Table 1) against body mass ($r = 0.856$), brain mass ($r = 0.898$) (Both data sets by Bauchot and Stephan (1969)), and constant of cephalization ($r = 0.902$) (Data by Hemmer (1971), based on the respective sets of body mass and brain mass)

development (Lanyon 1990). Just here is a crucial point in hominoid evolution, where quadrupedal gait changed to bipedal gait, or vice versa. Just skeletal structures that bear a direct functional relationship to body mass are to await to mislead in body mass estimation when the pattern of movement and the strains involved changed in that

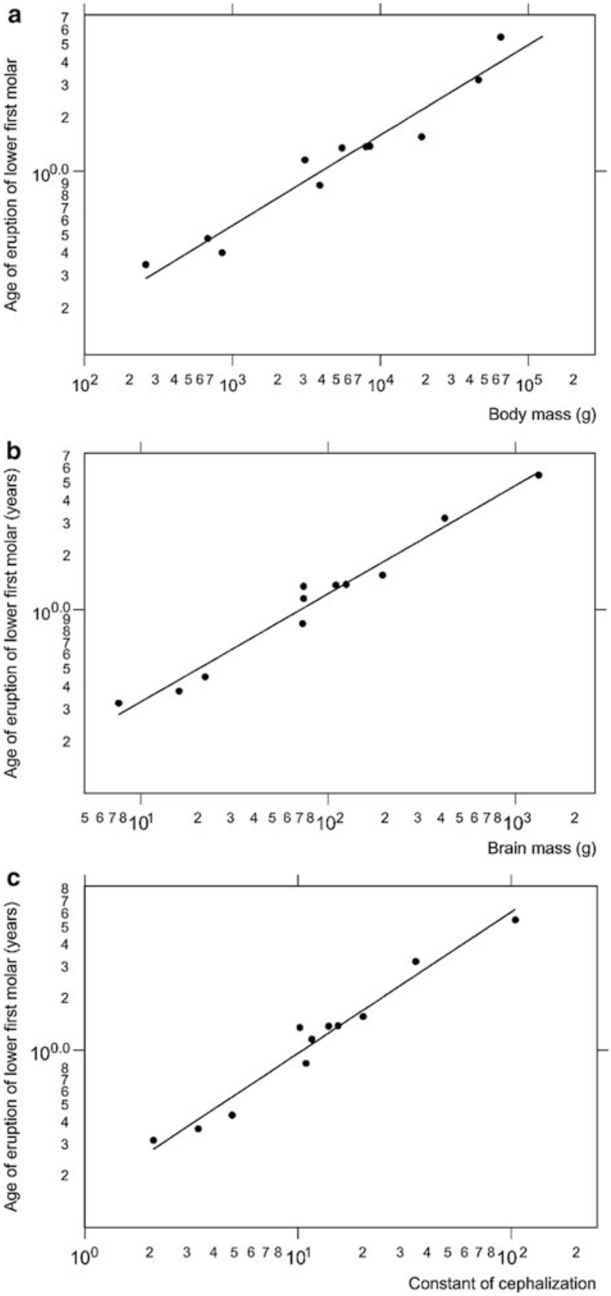


Fig. 2 Bivariate log–log plots (*lines*: least-squares regressions) of age of eruption of the lower first molar (Data by Smith (1989), with modifications by Smith et al. (1995)) against body mass ($r = 0.979$), brain mass ($r = 0.985$), and constant of cephalization ($r = 0.981$) (Data sources as for Fig. 1)

Table 5 Dental predictors of body mass (g) in primates, selected for $r \geq 0.95$

Dimension (mm ^{2})	r	Equation	Source and sample
Upper cheek tooth row length × width (CTL × CTW)	0.95	$\log BM = 2.06 \log(CTL \times CTW) - 1.00$	Martin (1990): 36 nonhuman species
P_3 crown area (length × width) (P_3CRA)	0.954	$\ln BM = 1.21 \ln P_3CRA + 1.21$	Gingerich et al. (1982): 43 nonhuman species
P_4 crown area (length × width) (P_4CRA)	0.955	$\ln BM = 1.44 \ln P_4CRA + 4.20$	Gingerich et al. (1982): 43 nonhuman species
M_1 crown area (length × width) (M_1CRA)	0.967	$\ln BM = 1.49 \ln M_1CRA + 3.55$	Gingerich et al. (1982): 43 nonhuman species
	0.99	$\ln BM = 1.572 \ln M_1CRA + 3.39$	Conroy (1987): 8 ape species
	0.96	$\ln BM = 1.570 \ln M_1CRA + 3.38$	Conroy (1987): 43 nonhuman anthropoid species
	0.96	$\ln BM = 1.438 \ln M_1CRA + 3.55$	Conroy (1987): 43 nonhuman anthropoid species, females
M_2 crown area (length × width) (M_2CRA)	0.968	$\ln BM = 1.31 \ln M_1CRA + 3.92$	Gingerich et al. (1982): 43 nonhuman species
Σ lower cheek teeth crown area (LCRA)	0.964	$\ln BM = 1.38 \ln LCRA + 1.67$	Gingerich et al. (1982): 43 nonhuman species

way. Predictor equations calculated for femoral diaphyseal diameters or circumferences, as well as for femoral articular dimensions (Jungers 1988, 1990; Kappelman 1996), and also for cross-sectional geometrical data, such as cortical area or area moments of inertia (Ruff 1990), lose their utility when developed with quadrupedal hominoids but are used for mass estimation in bipedal hominids [for convincing illustration of these issues, see Figs. 8.5, 8.7, and 8.8 in Ruff (1990) comparing femoral dimension allometric lines for *Homo sapiens* with those for pongids or nonhuman primates in general]. Mass estimates based on femoral dimensions of a bipedal hominoid using predictor equations developed with a nonhuman hominoid sample should thus be awaited not to meet the real values (44 % and 30 % overestimates for human males and females with a catarrhine femoral head diameter

Table 6 Cranial predictors of body mass (g) in primates, selected for $r \geq 0.95$

Dimension (mm)	r	Equation	Source and sample
Skull length (SL)	0.98	$\log BM = 3.89 \log SL - 4.09$	Martin (1990): 36 nonhuman species, MA
Bizygomatic width (BZ)	0.98	$\log BM = 3.77 \log BZ - 3.19$	Martin (1990): 36 nonhuman species, MA
Internal zygomatic length (IZ)	0.96	$\log BM = 3.26 \log IZ - 0.96$	Martin (1990): 36 nonhuman species, MA
Palate length (PAL)	0.96	$\log BM = 3.68 \log PAL - 2.08$	Martin (1990): 36 nonhuman species, MA
Occipital condyle area (OCCA) (LOCC × BOCC)	0.98	$\log BM = 2.16 \log OCCA$	Martin (1990): 36 nonhuman species, MA
	0.96	$\log BM = 1.61 \log OCCA - 1.00$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 1.68 \log OCCA - 0.87$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Occipital condyle length (LOCC)	0.96	$\log BM = 3.75 \log LOCC - 0.10$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 3.91 \log LOCC - 0.27$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Foramen magnum area (FMA)	0.98	$\log BM = 2.15 \log FMA - 1.20$	Martin (1990): 36 nonhuman species, MA
	0.97	$\log BM = 1.76 \log FMA - 0.28$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 1.81 \log FMA - 0.41$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Foramen magnum length (LFM)	0.96	$\log BM = 3.22 \log LFM$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 3.34 \log LFM - 0.15$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Foramen magnum breadth (BFM)	0.97	$\log BM = 3.83 \log BFM - 0.57$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 3.95 \log BFM - 0.70$	Aiello and Wood (1994): 23 simian species, both sexes, RMA

(*continued*)

Table 6 (continued)

Dimension (mm)	r	Equation	Source and sample
Orbital breadth (BORB)	0.96	log BM = 4.20 log BORB − 1.89	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		log BM = 4.38 log BORB − 2.14	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.96	log BM = 5.22 log BORB − 3.35	Aiello and Wood (1994): 6 hominoid species, both sexes, LSR
		log BM = 5.46 log BORB − 3.70	Aiello and Wood (1994): 6 hominoid species, both sexes, RMA
Orbital height (HORB)	0.95	log BM = 4.19 log HORB − 1.78	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		log BM = 4.40 log HORB − 2.14	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.98	log BM = 4.42 log HORB − 2.12	Aiello and Wood (1994): 6 hominoid species, both sexes, LSR
		log BM = 4.53 log HORB − 2.29	Aiello and Wood (1994): 6 hominoid species, both sexes, RMA
	0.961	log BM = 4.718 log HORB − 2.560	Kappelman (1996): 18 catarrhine sp. + ssp., both sexes, LSR
		log BM = 4.915 log HORB − 2.841	Kappelman (1996): 18 catarrhine sp. + ssp., both sexes, RMA
	0.957	log BM = 4.445 log HORB − 2.155	Kappelman (1996): 10 hominoid sp. + ssp., both sexes, LSR
		log BM = 4.657 log HORB − 2.472	Kappelman (1996): 10 hominoid sp. + ssp., both sexes, RMA

(*continued*)

Table 6 (continued)

Dimension (mm)	r	Equation	Source and sample
Orbital area (ORBA)	0.96	$\log BM = 2.14 \log ORBA - 1.94$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 2.22 \log ORBA - 2.16$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.98	$\log BM = 2.47 \log ORBA - 2.92$	Aiello and Wood (1994): 6 hominoid species, both sexes, LSR
		$\log BM = 2.52 \log ORBA - 3.05$	Aiello and Wood (1994): 6 hominoid species, both sexes, RMA
Orbital area, measured by computer digitizing (OA)	0.987	$\log BM = 2.284 \log OA - 2.239$	Kappelman (1996): 18 catarrhine sp. + ssp., both sexes, LSR
		$\log BM = 2.313 \log OA - 2.321$	Kappelman (1996): 18 catarrhine sp. + ssp., both sexes, RMA
	0.987	$\log BM = 2.258 \log OA - 2.176$	Kappelman (1996): 10 hominoid sp. + ssp., both sexes, LSR
		$\log BM = 2.287 \log OA - 2.261$	Kappelman (1996): 10 hominoid sp. + ssp., both sexes, RMA
Biorbital breadth (BIOR)	0.98	$\log BM = 3.85 \log BIOR - 2.81$	Aiello and Wood (1994): 23 simian species, both sexes, LSR
		$\log BM = 3.95 \log BIOR - 2.98$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.95	$\log BM = 4.82 \log BIOR - 4.67$	Aiello and Wood (1994): 6 hominoid species, both sexes, LSR
		$\log BM = 5.10 \log BIOR - 5.20$	Aiello and Wood (1994): 6 hominoid species, both sexes, RMA

(*continued*)

Table 6 (continued)

Dimension (mm)	*r*	Equation	Source and sample
Biporionic breadth (BPOR)	0.97	log BM = 3.32 log BPOR − 2.07	Aiello and Wood (1994): 23 simian species, both sexes, LSR
	0.98	log BM = 3.42 log BPOR − 2.25	Aiello and Wood (1994): 23 simian species, both sexes, RMA
		log BM = 3.77 log BPOR − 2.95	Aiello and Wood (1994): 6 hominoid species, both sexes, LSR
		log BM = 3.84 log BPOR − 3.10	Aiello and Wood (1994): 6 hominoid species, both sexes, RMA

LSR least-squares regression, *RMA* reduced major axis, *MA* major axis

regression (Kappelman 1996)). Femur-based estimates gained with the use of equations calculated with hominoids including man should be shifted somewhat more in the direction of the true values but still differ from them. In the case of using pure *Homo sapiens*-based predictor equations for body mass estimation in early hominids, caution needs to be exercised too, as all fossil hominids seem to have been characterized by considerable skeletal robusticity with thick long-bone cortices (Jungers 1988; McHenry 1992; Ruff and Walker 1993; Ruff et al. 1997).

If the fossil record of single *Homo* skeletons is complete enough to know the body height (stature) and width (bi-iliac breadth), relatively accurate body mass estimations will be possible based on these dimensions (Ruff and Walker 1993; Ruff et al. 1997; Table 8), provided that there are no basic differences in body proportions.

A crude approach to body mass of fossil hominoids other than simple comparisons among hominoid skeletons (for compilation of earlier trials of that type, see Suzman (1980)) may be done on the basis of close correlations of some cranial and postcranial dimensions with partial skeletal mass to represent body size (Steudel 1980). This procedure allows to compare fossils with the body mass of large, slightly larger than average, average, slightly smaller than average, or small male or female actual ape species. Approaches to body mass estimation in early hominids by a prediction of body height on the basis of postcranial elements and the subsequent use of a body height to body weight ratio (Wolpoff 1973) must meet the requirements of the same stature class, for which the ratio was calculated, and of the same limb-to-body proportions. Finally, another simplified attempt to estimate body mass of early hominids exclusively at the base of the cube of limb bone length or the square of diameter percentage deviations from a *Homo sapiens* standard skeleton (Krantz 1977) may not result in much more trustful body mass estimates than heavier, much heavier,

Table 7 Selection of postcranial predictors of body mass in hominoid primates, correlation coefficient ≥ 0.95

Dimension (mm)	r	Equation	Source and sample
12th thoracic vertebral body: AP × transverse diameter of the superior surface (THV)	0.968	$\log BM = 1.3782 \log THV - 2.3132$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 1.4244 \log THV - 2.4440$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.999	$\log BM = 0.6552 \log THV - 0.2443$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 0.6556 \log THV - 0.2456$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
5th lumbar vertebral body: AP × transverse diameter of the superior surface (LUV)	0.951	$\log BM = 1.3574 \log LUV - 2.4210$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 1.4277 \log LUV - 2.6288$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.983	$\log BM = 1.1593 \log LUV - 1.9630$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 1.1797 \log LUV - 2.0281$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA

(*continued*)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
Sacral body: AP × transverse diameter of the superior aspect (SAC)	0.968	$\log BM = 1.4991 \log SAC - 2.9735$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 1.5492 \log SAC - 3.1290$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
Humerus length [M1] (HLEN)	0.98	$\log \mathrm{BM} = 2.68 \log \mathrm{HLEN} - 1.94$	Aiello (1981): 23 anthropoid species, both sexes, LSR
	0.99	$\log \mathrm{BM} = 2.70 \log \mathrm{HLEN} - 2.02$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log \mathrm{BM} = 2.75 \log \mathrm{HLEN} - 2.15$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.95	$\log \mathrm{BM} = 3.59 \log \mathrm{HLEN} - 4.25$	Aiello and Wood (1994): 4 hominoid species, both sexes, LSR
		$\log \mathrm{BM} = 3.78 \log \mathrm{HLEN} - 4.74$	Aiello and Wood (1994): 4 hominoid species, both sexes, RMA
Humerus head AP diameter (HHAP)	0.985	$\log BM = 2.7018 \log HHAP - 2.6388$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 2.7431 \log HHAP - 2.7022$	McHenry (1992): 7 hominoid species, both sexes, RMA

(continued)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
Humerus midshaft circumference [M8] (HMSC)	0.98	log BM = 2.73 log HMSC − 0.27	Aiello (1981): 23 anthropoid species, both sexes, LSR
	0.96	log BM = 2.595 log HMSC − 0.113	Hartwig-Scherer (1993): African apes, 19 individuals, RMA
	0.98	log BM = 2.36 log HMSC − 0.16	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		log BM = 2.69 log HMSC − 0.25	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Humerus minimum circumference [M7] (HMIN)	0.98	log BM = 2.67 log HMIN − 0.18	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		log BM = 2.73 log HMIN − 0.27	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Humerus distal epiphyseal breadth [M4] (HEPI)	0.98	log BM = 2.49 log HEPI + 0.26	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		log BM = 2.56 log HEPI + 0.17	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.95	log BM = 2.72 log HEPI − 0.20	Aiello and Wood (1994): 4 hominoid species, both sexes, LSR
		log BM = 2.88 log HEPI − 0.48	Aiello and Wood (1994): 4 hominoid species, both sexes, RMA

(*continued*)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
Humerus distal joint breadth (HDJT)	0.98	$\log BM = 2.44 \log HDJT + 0.70$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log BM = 2.49 \log HDJT + 0.63$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Humerus distal: capitular height × articular width (ELB)	0.966	$\log BM = 1.4115 \log ELB - 2.4855$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 1.4617 \log ELB - 2.6280$	McHenry (1992): 7 hominoid species, both sexes, RMA
Radius head mediolateral diameter (RADH)	0.955	$\log BM = 1.9910 \log RADH - 0.8912$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 2.0859 \log RADH - 1.0132$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
Radius midshaft circumference (RMSC)	0.97	$\log BM = 2.826 \log RMSC + 0.031$	Hartwig-Scherer (1993): African apes, 19 individuals, RMA
Acetabular capacity (cm^3) (ACCA)	0.987	$BM = 4.162\ ACCA - 2.541$	Suzman (1980): 7 chimpanzees
	0.967	$BM = 3.842\ ACCA - 28.031$	Suzman (1980): 6 gorillas
Acetabulum height (ACET)	0.967	$\ln BM = 2.8025 \ln ACET - 6.6459$	Jungers (1988): 7 hominoid species, both sexes
	0.997	$\ln BM = 3.1824 \ln ACET - 7.9090$	Jungers (1988): 6 nonhuman hominoid species, both sexes

(*continued*)

Table 7 (continued)

Dimension (mm)	r	Equation	Source and sample
Femur length (FL)	0.987	$\log BM = 3.498 \log FL - 6.750$	Ruff (1990): 4 nonhuman anthropoid species, both sexes
Femur head AP diameter [M19.3] (APFH)	0.98	$\mathrm{log\ BM} = 2.45\ \mathrm{log\ APFH} + 0.92$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\mathrm{log\ BM} = 2.50\ \mathrm{log\ APFH} + 0.86$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.98	$BM = 2.239\ APFH - 36.5$	Ruff et al. (1997): modern *Homo sapiens* sample
Femur head vertical diameter [M18] (VDFH)	0.970	$\log BM = 2.6465 \log VDFH - 2.4093$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 2.7284 \log VDFH - 2.5310$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.976	$\log BM = 1.7125 \log VDFH - 1.0480$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 1.7538 \log VDFH - 1.1137$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
	0.98	$\mathrm{log\ BM} = 2.44\ \mathrm{log\ VDFH} + 0.95$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR

(continued)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
		$\log BM = 2.53 \log VDFH + 0.83$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.988	$\log BM = 2.466 \log VDFH + 0.913$	Kappelman (1996): 14 catarrhine sp. + ssp., mostly both sexes, LSR
		$\log BM = 2.497 \log VDFH + 0.872$	Kappelman (1996): 14 catarrhine sp. + ssp., mostly both sexes, RMA
	0.996	$\log BM = 2.628 \log VDFH + 0.718$	Kappelman (1996): 13 catarrhine sp. + ssp., mostly both sexes, without *Homo*, LSR
		$\log BM = 2.640 \log VDFH + 0.702$	Kappelman (1996): 13 catarrhine sp. + ssp., mostly both sexes, without *Homo*, RMA
Femur head diameter (FHD)	0.974	$ln\ BM = 2.6142\ ln\ FHD - 5.4282$	Jungers (1988): 7 hominoid species, both sexes
	0.997	$ln\ BM = 2.9047\ ln\ FHD - 6.3233$	Jungers (1988): 6 nonhuman hominoid species, both sexes
Femur shaft AP × transverse diameter inferior to the lesser trochanter [M9 × M10] (FS)	0.973	$log\ BM = 1.1823\ log\ FS - 1.5745$	McHenry (1992): 7 hominoid species, both sexes, LSR

(continued)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
		$\log BM = 1.2152 \log FS - 1.6605$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.978	$\log BM = 0.7927 \log FS - 0.5233$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 0.8107 \log FS - 0.5733$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
		$\log \mathrm{BM} = 1.475 \log \mathrm{FS} + 0.524$	Hartwig-Scherer (1993): African apes, 19 individuals, RMA
Femur shaft circumference inferior the lesser trochanter (FSC)	0.95	$\log \mathrm{BM} = 2.862 \log \mathrm{FSC} - 0.779$	Hartwig-Scherer (1993): African apes, 19 individuals, RMA
Femur midshaft transverse diameter (FMTD)	0.99	$\log \mathrm{BM} = 2.55 \log \mathrm{FMTD} + 1.19$	Aiello (1981): 23 anthropoid species, both sexes, LSR
	0.981	$\log BM = 2.492 \log FMTD - 1.696$	Ruff (1990): 5 anthropoid species, both sexes
	0.982	$\log BM = 2.533 \log FMTD - 1.737$	Ruff (1990): 4 nonhuman anthropoid species, both sexes
	0.969	$\log BM = 2.541 \log FMTD - 1.793$	Ruff (1990): African apes and human, both sexes
Femur midshaft circumference [M8] (FMSC)	0.98	$\log \mathrm{BM} = 2.64 \log \mathrm{FMSC} - 0.29$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR

(*continued*)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
		$\log BM = 2.71 \log FMSC - 0.39$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
	0.95	$\log BM = 2.809 \log FMSC - 0.597$	Hartwig-Scherer (1993): African apes, 19 individuals, RMA
Femur biepicondylar × distal shaft AP diameter (FDIST)	0.961	$log\ BM = 1.0829\ log\ FDIST - 1.8467$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$log\ BM = 1.1271\ log\ FDIST - 1.9840$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.968	$log\ BM = 0.9600\ log\ FDIST - 1.5678$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$log\ BM = 0.9921\ log\ FDIST - 1.6762$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
Femur epicondylar breadth [M21] (FEPIML)	0.98	$\log BM = 2.48 \log FEPIML + 0.29$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log BM = 2.53 \log FEPIML + 0.21$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Femur epicondylar depth [M24] (FEPIAP)	0.97	$\log BM = 2.59 \log FEPIAP + 0.28$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log BM = 2.66 \log FEPIAP + 0.18$	Aiello and Wood (1994): 23 simian species, both sexes, RMA

(*continued*)

Table 7 (continued)

Dimension (mm)	*r*	Equation	Source and sample
Femur medial condyle posterior width (MCW)	0.978	$\ln BM = 2.1224 \ln MCW - 2.6824$	Jungers (1988): 7 hominoid species, both sexes
	0.979	$\ln BM = 2.1743 \ln MCW - 2.8023$	Jungers (1988): 6 nonhuman hominoid species, both sexes
Femur lateral condyle posterior width (LCW)	0.950	$\ln BM = 1.9335 \ln LCW - 1.7269$	Jungers (1988): 7 hominoid species, both sexes
	0.977	$\ln BM = 2.1865 \ln LCW - 2.3033$	Jungers (1988): 6 nonhuman hominoid species, both sexes
Tibia length (TL)	0.981	$\log BM = 4.123 \log TL - 7.914$	Ruff (1990): 4 nonhuman anthropoid species, both sexes
Tibia proximal AP × transverse diameter (TPR)	0.973	$\log BM = 1.2770 \log TPR - 2.5918$	McHenry (1992): 7 hominoid species, both sexes, LSR
		$\log BM = 1.3127 \log TPR - 2.7066$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.991	$\log BM = 1.0583 \log TPR - 1.9537$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 1.0683 \log TPR - 1.9880$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RM
Tibia distal AP × transverse diameter of the talar facet (TDIST)	0.965	$\log BM = 1.1806 \log TDIST - 1.5390$	McHenry (1992): 7 hominoid species, both sexes, LSR

(*continued*)

Table 7 (continued)

Dimension (mm)	r	Equation	Source and sample
		$\log BM = 1.2232 \log TDIST - 1.6493$	McHenry (1992): 7 hominoid species, both sexes, RMA
	0.991	$\log BM = 0.9005 \log TDIST - 0.8790$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, LSR
		$\log BM = 0.9246 \log TDIST - 0.9743$	McHenry (1992): *Homo sapiens*, both sexes, 3 populations, RMA
Tibia midshaft circumference [M10] (TMSC)	0.97	$\log \mathrm{BM} = 2.84 \log \mathrm{TMSC} - 0.43$	Aiello and Wood (1994): 20 simian samples, LSR
		$\log \mathrm{BM} = 2.92 \log \mathrm{TMSC} - 0.94$	Aiello and Wood (1994): 20 simian samples, RMA
Medial tibial plateau AP diameter [M4a] (TMED)	0.96	$\log \mathrm{BM} = 2.48 \log \mathrm{TMED} + 0.88$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log \mathrm{BM} = 2.60 \log \mathrm{TMED} + 0.74$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Lateral tibial plateau AP diameter (TLAT)	0.95	$\log \mathrm{BM} = 2.63 \log \mathrm{TLAT} + 0.79$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR
		$\log \mathrm{BM} = 2.76 \log \mathrm{TLAT} + 0.62$	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Tibia proximal breadth [M3] (TPROX)	0.98	$\log \mathrm{BM} = 2.45 \log \mathrm{TPROX} + 0.35$	Aiello and Wood (1994): 21 simian species (17: both sexes), LSR

(*continued*)

Table 7 (continued)

Dimension (mm)	r	Equation	Source and sample
		log BM = 2.51 log TPROX + 0.26	Aiello and Wood (1994): 23 simian species, both sexes, RMA
Distal tibial articulation AP diameter (DTB)	0.957	*ln BM = 2.5037 ln DTB − 3.9397*	Jungers (1988): 7 hominoid species, both sexes
	0.988	*ln BM = 2.8561 ln DTB − 4.8747*	Jungers (1988): 6 nonhuman hominoid species, both sexes

Dimensions in mm (or mm^2); numbers in square brackets refer to measurements numbers in Martin (Martin and Saller 1959). Body mass in g; equations in italics, body mass in kg
LSR least-squares regression, *RMA* reduced major axis

Table 8 Body mass prediction based on stature and bi-iliac breadth

Equation	r	Source and sample
BM = 0.413 ST + 2.892 BI − 84.8	0.941	Ruff and Walker (1993): 21 males, worldwide adult population
BM = 0.498 ST + 1.877 BI − 74.6	0.965	Ruff and Walker (1993): 306 male Karkar Islanders, 8–67 years
BM = 0.373 ST + 3.033 BI − 82.5	0.90	Ruff et al. (1997): males

Only samples with $r \geq 0.90$ were selected
BM body mass (kg), *ST* stature (cm), *BI* bi-iliac breadth (cm): before applying these formulas, skeletal bi-iliac breadth is converted to living bi-iliac breadth using the equation living BI = 1.17 skeletal BI − 3 (Ruff et al. 1997)

lighter, or much lighter compared to the standard, as such a procedure neglects size-dependent allometric shifts and evolutionary changes in body proportions.

It should always be kept in mind that body mass estimates resulting from either cranial or postcranial variables are subject to considerable error (Jungers 1990; Martin 1990; Ruff and Walker 1993; Aiello and Wood 1994; Kappelman 1996). Given this fact (Table 5) and the use of equations based on highly correlating samples ($r \geq 0.95$; the correlation coefficient depends on the overall size variability and allows for higher values in all primate samples than in taxon-specific samples, but the latter otherwise may have a higher misleading potential for predicting equations used for extinct species), different available line-fitting techniques to create predicting equations (least-squares regression, reduced major axis, major axis) and the partial availability of correction factors to compensate for bias, introduced when a body mass estimate derived in logarithmic units is detransformed back to arithmetic units (Smith 1993), as well as many other issues around estimation of body mass in paleontology

(Smith 2002), may not really merit that high attention for practical use as sometimes postulated (Gingerich et al. 1982; McHenry 1992; Hartwig- Scherer 1993; Aiello and Wood 1994; Kappelman 1996). Individual body mass estimates of fossil specimens of course may be calculated that are mathematically quite correct, even to the nearest 100 g, for further statistical use; but nevertheless, it is biologically wise to list them not in that accurate form but as roughly rounded values. To give a comparable example, rounding to the nearest kilogram was proposed for body mass prediction in fossil cats only for specimens weighing less than 20 kg; rounding to the nearest 5 kg, for the range between 20 and 50 kg; and rounding to the nearest 10 kg, for specimens weighing more than 50 kg (Hemmer 2004).

Estimating Brain Mass

Cranial capacities measured in cm^3 are not the same as brain masses measured in g. In primates, the general relationship will be cranial capacity > brain mass > brain volume (Smith et al. 1995). Unfortunately, this is not always done in comparative publications [e.g., cranial capacities labeled brain mass in Table 1 of Harvey and Clutton-Brock (1985), identical with Table 15.1 of Harvey et al. (1987); see Smith et al. 1995]. There is also no stable relationship between brain mass and cranial capacity [e.g., 1/1.05 as used for humans by different authors (Smith et al. 1995) or 1/1.14 as used by Hartwig-Scherer (1993), following Count (1947)] over the whole range of brain size variability. The repeatedly found allometric exponent of 1.02 (Martin (1990), for primates; Röhrs and Ebinger (2001), for mammals other than primates) does not mean an isometric relationship between the two variables at correlation coefficients as high as 0.995–0.997 (Table 9). Therefore, all comparative work using brain size should either center on cranial capacities or brain masses. Calculations of relative brain size (cephalization, encephalization quotient) based on body mass clearly should proceed with brain mass. Unfortunately, the available predictive equations for primates or mammals in general give quite differing brain mass values (Table 10). The primate cranial capacity brain mass conversion formula (Martin 1990) is retained here, since it produces neither clearly excessive values in the upper (*Homo sapiens*) range in view of such conversion data as presented by earlier authors [compilation in Martin and Saller (1959)] nor nonsense values in the lower range, whereby brain volumes would become just larger than cranial capacities (as produced with the use of the formula of Ruff et al. (1997)).

It should be noted that there are some pitfalls in the determination of the cranial capacity as basis for brain mass estimation. The usual method of packing the cranial cavity with small rounded particles as lead shot, mustard seed or millet grain, and other comparable materials is limited by the need to condense the fill both in the skull and in the measuring cylinder in the same way. The method closing the foramina before packing the cranial cavity may also influence the result. A good standardized practice is needed to achieve a tolerable accuracy with this volumetric approach, and it may be combined with a weighing procedure (Smith et al. 1995). Measurements obtained by the packing method may surpass the volume of artificial

Table 9 Interspecific allometric relationship of cranial capacity and brain mass in primates and in mammals other than primates

Sample	Allometric equation	r	Authors	Formula converted for mass estimation
33 primate species	$CrC = 0.94\ BrM^{1.02}$	0.996	Martin (1990, p 363 + Fig. 8.4)	$\log BrM = 0.98 \log CrC + 0.0246$
27 primate species	–	0.995	Ruff et al. (1997)	$\log BrM = 0.976 \log CrC + 0.0596$
17 mammal species	$CrC = 0.96\ BrM^{1.02}$	0.997	Röhrs and Ebinger (2001)*	$\log BrM = 0.98 \log CrC + 0.0168$

BrM brain mass, *CrC* cranial capacity (cm^3)

[a] The authors present this equation as $\log CrC = -0.0015 + 1.02 \log BrV$ (BrV = brain volume) and add the equation BrV = BrM:1.036

Table 10 Cranial capacity-based brain mass estimates (g) by the use of different equations (Table 9)

Cranial capacity (cm^3)	Brain mass estimated by the primate formula of Martin (1990)	Brain mass estimated by the primate formula of Ruff et al. (1997)	Brain mass estimated by the mammalian formula of Röhrs and Ebinger (2001)
50	49	52	48
100	97	103	95
500	467	494	459
1,000	922	972	905
1,500	1,371	1,444	1,347

endocasts (Martin 1990, Table 8.5: 10–11 % in the Eocene lemuroid primate *Adapis parisiensis*). The estimation of endocranial volume by double graphic integration derived from X-ray pictures may result in substantially diverging values (Martin 1990, Table 8.5: 10–12 % less than the artificial endocast in *Adapis parisiensis*). An assessment of cranial capacity in fossil primates also may be done by the use of linear cranial dimensions (Martin 1990; Table 11).

Calculating Relative Brain Size

There are four main concepts of scaling relative brain size in primates (McHenry 1976). The constant of cephalization (CC) (Hemmer 1971) was developed on the base of a common mammalian intraspecific allometric exponent around 0.23 [$BrM = CC \times BM^{0.23}$; BrM = brain mass (g), BM = body mass (g)]. The index of progression (IP) (Bauchot and Stephan 1966, 1969) gives the ratio of actual brain mass to brain mass predicted on the basis of an interspecific basal insectivore allometric equation with an exponent of 0.63. [The index of cranial capacity (ICC)

Table 11 Estimation of cranial capacity (CrC) (cm^3) by linear dimensions in primates (Martin 1990: Table 8.10)

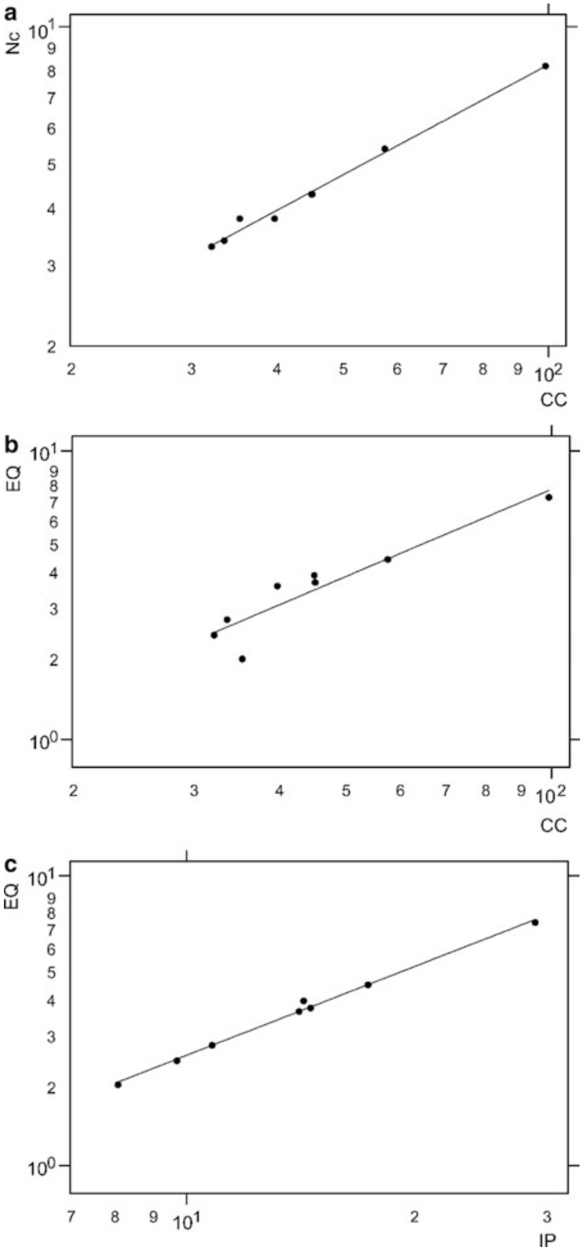
Dimension (mm)	*r*	Equation
Braincase width (CW)	0.99	$\log CrC = 3.24 \log CW - 3.75$
Braincase height (CH)	0.98	$\log CrC = 2.91 \log CH - 2.91$
Braincase length (CL)	0.98	$\log CrC = 3.28 \log CL - 4.37$
Sum CW + CH + CL (SU)	0.995	$\log CrC = 3.12 \log SU - 5.18$
Product CW × CH × CL (PR)	0.995	$\log CrC = 1.02 \log PR - 3.54$

The formulas are based on the major axis, and the cranial capacities were determined by packing the cranial cavity with sintered glass particles

as introduced by Martin (1990) follows just the same lines as the index of progression.] The encephalization quotient (EQ) (Jerison 1973) is also the ratio of actual to predicted brain mass, the latter based on an interspecific mammalian allometry (predicted brain mass $= 0.12\ BM^{2/3}$). The extra-neuron count (Nc) (Jerison 1973) "is a numerical measure of progressiveness in brain development beyond the level required by increasing body size" (Jerison 1973). The results of the CC and Nc methods perfectly correlate on the one hand as do the results of the IP and EQ methods on the other (Fig. 3). This reduces the issues on principle to the choice of either the intraspecific (CC and Nc methods) or the interspecific (IP and EQ) type of brain to body mass allometries.

EQ has been widely used in the last three decades by the overwhelming majority of authors (Hartwig-Scherer 1993; Kappelman 1996; Ruff et al. 1997; McHenry and Coffing 2000). The results of EQ calculations vary depending on which of the different equations is selected (Kappelman 1996) [allometric exponents varying from 0.60 (Old World simian EQ: Martin 1990) or 0.67 (Jerison 1973) close to 0.75 (0.74–0.76) (Martin 1990; Hartwig-Scherer 1993; Ruff et al. 1997; McHenry and Coffing 2000)]. Nevertheless, some writers have begun to feel uncomfortable about the EQ method (McHenry 1988; Kappelman 1996; Arsuaga et al. 1999; Rightmire 2004). A negative allometric relationship between body size and EQ was raised, but the reasons were assumed to be unclear (Kappelman 1996). EQ being a function of body mass predicted for individuals using an interspecific equation, the comparison of EQ values determined for fossils was considered to be misleading (Rightmire 2004). Similarly, the EQ was not felt to be meaningful when closely related species with widely differing body mass are compared (Arsuaga et al. 1999). Curious EQ results like a position of *Miopithecus talapoin* above all nonhuman hominoids, the gorilla ranging below all cercopithecines (Hemmer 1971; Table 2), or *Cebus albifrons* lying between *Homo erectus* and *Homo sapiens* (Hartwig-Scherer 1993, Fig. 6) also indicate that this procedure may be seriously biologically inadequate. All such problems disappear when the CC intraspecific approach is followed instead of the EQ interspecific method (Hemmer 1971). As a by-effect of the low intraspecific allometric exponent, the influence of differences in body mass predictions on EQ calculations (Conroy 1987) is less profound with the CC method.

Fig. 3 Bivariate log-log plots (*lines*: least-squares regressions) to demonstrate the mutual relationship of the main methods to scale relative brain size (Data from McHenry (1976), Table 2; hominoid primates). (**a**) Extra-neuron count (*Nc*) (Jerison 1973) against constant of cephalization (*CC*) (Hemmer 1971) ($r = 0.997$). (**b**) Encephalization quotient (*EQ*) (Jerison 1973) against constant of cephalization (*CC*) $r = 0.971$). (**c**) Encephalization quotient (*EQ*) against index of progression (*IP*) (Bauchot and Stephan 1966) ($r = 0.998$)



Life History Data Estimations in Fossil Hominids

The final approach to life history data estimation in fossil hominoids, especially in fossil hominids, is a story of reliability of the prediction equations to be used. There is a wide variability in the results of body mass estimation obtained on the basis of different species samples used to create the equations, on the basis of different dimensions, and using different line-fitting techniques (Table 12). The availability of several parts of a single skeleton, as, e.g., in the female *Australopithecus afarensis* AL 288-1 specimen, allows for many independent estimates, which group together centrally to resemble a normal distribution, to give a clear and conclusive view of the most probable body mass of that individual and to allow easy recognition of outsider values (Fig. 4). In the AL 288-1 case, the peak of the density curve (made up of 54 estimates) is found near 29 kg, and the mean and the median range near 30 kg, allowing for a consistent estimation of body mass roughly around 30 kg, as also found in earlier studies (Jungers 1988, 1990; McHenry 1992). The existence of such a key specimen also allows us to judge empirically which predictors may be more useful and which should be excluded from the estimation process for a taxon for which neither humans nor African apes are completely adequate models (Hartwig-Scherer 1993). For AL 288-1, dimensions of the humerus and radius heads and the elbow joint (McHenry 1992) produce clearly estimates that are too small based on general hominoid allometries as does the size of the sacral body (McHenry 1992). On the other hand, very large estimates result from the circumference of the humerus based on *Homo sapiens* allometry and from the circumference of the tibia based on an African ape allometry (Hartwig-Scherer 1993), while the dentition provides an outsider value (Jungers 1988).

The availability of well-founded body mass estimates based on postcranial predictors allows us to determine which cranial predictors compare in reliability with them for *Australopithecus* and early *Homo* as well. Orbital height was extracted as the cranial variable which produces body mass estimates that are most in line with postcranially generated estimates (Aiello and Wood 1994). This may be supplemented by estimates based on a computer digitizing measurement of the orbital area (Kappelman 1996).

Published body mass estimates based on these cranial dimensions were used together with most relevant postcranially predicted data to extract rounded mean body mass for *Australopithecus* and *Homo* paleopopulations and to calculate in each case the CC with rounded mean brain mass converted from mean cranial capacity (Tables 13 and 14). These brain mass and CC data were then used as the source material for the estimation of life history traits. The evaluation of the reliability of the life history trait predictor equations (Tables 3 and 4) was done empirically based on the PE of the estimation of *Homo sapiens* [PE $=$ (observed $-$ predicted)/predicted $\times$ 100]. Only equations with a PE ≤ 5 % were considered to be useful for the life history estimation in fossil hominids. It must never be forgotten that most of the actually observed primate life history dimensions are subject to enormous variability produced by diverse ecological factors. Any prediction for extinct populations will be subject to this variability too.

Table 12 Selected examples that characterize the broad variability of body mass estimates (kg) of fossil hominids derived at the base of different predicting equations

Species and specimen	Body mass predicted by dental dimensions	Body mass predicted by cranial dimensions	Body mass predicted by postcranial dimensions	Source
Australopithecus afarensis AL 288-1	52.8		30.4–30.4, 27.4–29.6, 32.3–36.0, 32.2–35.5, 24.3–26.2, 26.3–28.5, 35.1–39.8, 38.9–29.9, 17.4-17.1-17.3–27.3-25.9-26.5, 16.5-16.0-16.1-30.7-30.0-29.9, 12.9-11.8-12.3–28.2-27.1-27.5, 24.1-23.6-23.7–32.5-32.5-32.5, 28.5-27.4-27.7-17.0-16.2-16.4, 27.9-27.6-27.7–27.9-27.4-27.6, 35.2-35.3-35.2–37.1-36.9-36.9, 32.2-32.2-32.2–27.8-27.7-27.7, 27.1-26.9-26.9–24.4-24.1-24.0, 37.0-36.8-36.9–27.6-26.1-26.6, 23.5, 29–30, 27, 26–41, 23–35, 34–34, 32–27, 34–26, 30, 41–31	Jungers (1988, 1990), McHenry (1988), McHenry (1992), Ruff and Walker (1993), Hartwig-Scherer (1993)
A. (*Paranthropus*) *boisei* KNM-ER 406		66.6–64.4–59.8–60.1, 57.6–58.8–61.3–60.7, 92.3–96.9–85.8–85.4, 69.8		Aiello and Wood (1994), Kappelman (1996)
Homo sp. (*rudolfensis*) [*Australopithecus* (*Paranthropus*) *boisei* ?] KNM-ER 1481			84.0-88.4-86.4–57.0-57.4-57.3, 50.3–48.7–57.1-58.2-58.0–51.3-51.4-51.4, 66.3-68.4-68.2–48.3-48.4-48.3, 54.9-55.9-	McHenry (1988), McHenry 1992, Ruff and Walker (1993), Hartwig-Scherer (1993)

(*continued*)

Table 12 (continued)

Species and specimen	Body mass predicted by dental dimensions	Body mass predicted by cranial dimensions	Body mass predicted by postcranial dimensions	Source
			55.7–43.2-43.2-43.2, 55.8-57.1-56.9–42.4-42.3-42.3, 46, 58.4, 86.9–106.5, 45–41, 48–36, 50–35, 43	
Homo sp. *rudolfensis* KNM-ER 1470		80.4–77.4–70.5–70.6, 50.7–51.9–54.2–53.9, 95.2–99.8–88.1–87.7, 45.6		Aiello and Wood (1994), Kappelman (1996)

Mass estimates separated by "-": prediction based on the same dimension and the same species sample but different line-fitting technique; mass estimates separated by "–": prediction based on the same dimension but different species samples; mass estimates separated by ",": prediction based on different dimensions

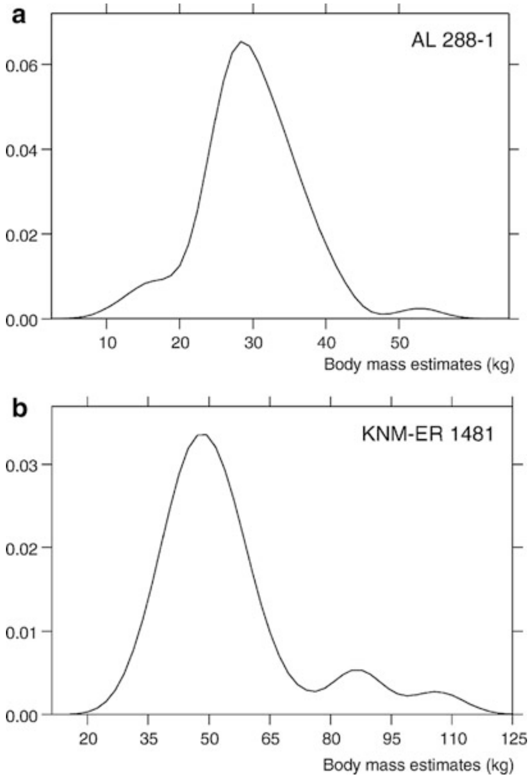


Fig. 4 Density curves of the distributions of body mass estimates in selected examples of early hominid specimens, based on published values as given in Table 12 (mean values when there are two or three different values based on the same dimension and the same species sample but different line-fitting techniques) (Plots created by use of MathSoft Axum 6.0)

Table 13 Estimates of body mass, brain mass, and constant of cephalization in ***Sahelanthropus*** and ***Australopithecus***

Taxon	Sex	Body mass, cranial estimate (kg)		Body mass, postcranial estimate (kg)		Retained body mass (kg)
		a	b	c	d	
Sahelanthropus tchadensis	Male?	58[e]				**c.58**
Australopithecus afarensis	Male				45	**c.45**
	Female				29	**c.30**
	Both sexes			30–68		**c.40**
Australopithecus africanus	Male				41	**c.40**
	Female	30, 22	27, 28		30	**c.30**
	Both sexes			33–58		**c.35**
A. (*Paranthropus*) *aethiopicus*	Male		38			**c.40**
A. (*Paranthropus*) *boisei*	Male	58,39	70, 58		49	**c.50**
	Female	26	32		34	**c.30**
	Both sexes			45–51		**c.40–45**
A. (*Paranthropus*) *robustus*	Male				40	**c.40**
	Female				32	**c.30**
	Both sexes		47	37–56		**c.35–40**

Original body mass values rounded to the next kg and retained body mass to the next 5 kg. Brain mass estimated on the basis of the formula given by Martin (1990, Table 9) and retained brain mass rounded to the next 5 g

[a] Aiello and Wood (1994, mean of LSR and RMA estimates)

[b] Kappelman (1996)

[c] Jungers (1988)

[d] McHenry and Coffing (2000)

[e] Basic dimensions by Brunet et al. (2002): orbital height used to estimate body mass with equations (Table 6) published by Aiello and Wood (1994) and Kappelman (1996)

Taxon	Cranial capacity (cm^3)		Brain mass estimate (g)		Retained brain mass (g)	Constant of cephalization
	b	d				
Sahelanthropus tchadensis	c.320–380[e]		302–357		**c.300–360**	**c.24–29**
Australopithecus afarensis						
		434		407	**c.405**	**c.35**
Australopithecus africanus						**c.40**
	428, 485		401, 454		**c.430**	
		452		423	**c.425**	**c.38**
A. (*Paranthropus*) *aethiopicus*	410		385		**c.385**	**c.34**
A. (*Paranthropus*) *boisei*	510, 530		476,495			
	500		467			
		521		487	**c.485**	**c.42**
A. (*Paranthropus*) *robustus*						
		530		495	**495**	**c.44**

Table 14 Estimates of body mass, brain mass, and constant of cephalization in Pleistocene ***Homo***

Taxon	Sex or specimen	Body mass, cranial estimate (kg)		Body mass, postcranial estimate (kg)		Retained body mass (kg)
		a	b	c	d	
Homo sp. *habilis*, earliest Pleistocene	Male			37		**c.35**
	Female	34, 26	30, 35	32		**c.30**
	Both sexes					**c.35**
Homo sp. *rudolfensis*, earliest Pleistocene	KNM-ER 1470	51	47			**c.50**
	Both sexes			51–60		
Homo sp. *georgicus*, Early Pleistocene	Female		30[e]			**c.30**
	Both sexes					
Homo sp. *ergaster*, Early Pleistocene	Both sexes	58–66	57–60	56–66		**c.60**
Homo sp. *erectus*, Early Middle Pleistocene	Zhoukoudian XI		52			
	Zhoukoudian XII		66			
	Sangiran 17	58	76			
	Both sexes					**c.60**
Archaic *Homo sapiens*, Middle Pleistocene, Europe	Arago	35[f]				
	Sima d.l. Huesos	94[g]				
	Steinheim	35[f]	61			
	Petralona	52[f]				
	Both sexes					**c.55**
Late archaic *Homo sapiens* (Neanderthals)	Male	81–100	92			**c.90**
	Both sexes				76	**c.75**

Original body mass values rounded to the next kg and retained body mass to the next 5 kg. Brain mass estimated on the basis of the formula given by Martin (1990, Table 9) and retained brain mass rounded to the next 5 g

[a] Aiello and Wood (1994, mean of LSR and RMA estimates)

[b] Kappelman (1996)

[c] McHenry and Coffing (2000)

[d] Ruff et al. (1997)

[e] Basic dimensions of skull D 2700 by Vekua et al. (2002): orbital height used to estimate body mass with equations (Table 6) published by Aiello and Wood (1994) and Kappelman (1996); additional cranial capacities of D 2280 and D 2282 by Gabunia et al. (2000)

[f] Rightmire (2004)

[g] Arsuaga et al. (1999)

Taxon	Cranial capacity (cm^3)		Brain mass estimate (g)		Retained brain mass (g)	Constant of cephalization
	b	c				
Homo sp. *habilis*, earliest Pleistocene						
	594, 509		553, 476		**c.515**	**c.48**
		612		570	**c.570**	**c.51**
Homo sp. *rudolfensis*, earliest Pleistocene	752		697		**c.695**	**c.58**
Homo sp. *georgicus*, Early Pleistocene	c.600[e]		c.559		**c.560**	**c.52**
	675		627		**c.625**	
Homo sp. *ergaster*, Early Pleistocene	804–909	871	744–839	805	**c.805**	**c.64**
Homo sp. *erectus*, Early Middle Pleistocene	1,015		935			
	1,030		949			
	1,004		925			
					c.935	**74**
Archaic *Homo sapiens*, Middle Pleistocene, Europe	1,166[f]		1,071			
	1,390[g]		1,273			
	1,100[f]		1,012			
	1,230[f]		1,129			
					c.1120	**c.91**
Late archaic *Homo sapiens* (Neanderthals)	1,565		1,430		**c.1430**	**c.104**
	1,489[d]		1,370		**c.1370**	**c.104**

Table 15 Estimations of life history data in ***Sahelanthropus***, ***Australopithecus***, and ***Homo*** fossil samples

Taxon	Age at eruption of the first lower molar (years)	Age at sexual maturity, female (years)	Age at first breeding, female (years)	Maximum life span (years)
Gorilla gorilla	–	6.5	9.9	39.3
Pan troglodytes	3.15	9.8	11.5	44.5
Sahelanthropus tchadensis	≥2¼ ≤2½	≥6 ≤8	≥8 ≤10	≥38 ≤ 44
Australopithecus afarensis	2¾	8	10½	45
Australopithecus africanus	3	8½	11	46
Australopithecus boisei	3	9	11½	48
Australopithecus robustus	3	9	11½	49
Homo sp. *habilis*	3¼–3½	9½–10	12–12½	50–51
Homo sp. *rudolfensis*	3¾	11	14	55
Homo sp. *georgicus*	3½	10–10½	13	51–54
Homo sp. *ergaster*	4¼	12	15	57
Homo sp. *erectus*	4½	13	16	60
Archaic *Homo sapiens*, Europe	5	14½	18	65
Homo sapiens, Neanderthals	5¾	16	19½	69
Homo sapiens, observed values	5.4	16.5	19.3	70

Age at eruption of the first lower molar rounded to the next ¼ years, age at sexual maturity and at first breeding rounded to the next ½ year, and maximum life span rounded to the next year. All estimations based on the predictor equations evaluated as useful or very useful (Tables 3 and 4) (mean predicted value, if more than one equation per dimension meets the criteria). The actual observed *Gorilla gorilla*, *Pan troglodytes*, and *Homo sapiens* values are those used for the calculations of the predictor equations [Published by Smith et al. (1995) (molar eruption) and Harvey and Clutton-Brock (1985)]

Nevertheless, the results then obtained confirm, correct, and supplement the earlier [Hemmer (1974) on the age at sexual maturity, at first breeding, and at teeth eruption in *Australopithecus*] and later calculations [Smith and Tompkins (1995) on first permanent molar eruption]. At the same time, they are supported by results of osteobiographic techniques. *Australopithecus* (*afarensis*, *africanus*, *robustus*) and early *Homo* specimens, aged at something like 3–3.5 years on the basis of incisor crowns with little or no root development, had first permanent molars coming into occlusion (Bromage 1990) just as predicted with first lower molar eruption at around 3 years (Table 15). The estimation of life history data confirms the fundamental nature of the australopithecines as progressive apes, not as humans, the early *Australopithecus afarensis* ranging within the modern African ape life history dimensions.

Some important new fossil taxa discovered in the last years are included in the selected samples of life history data presentation (Table 15). The interpretation of the Late Miocene *Sahelanthropus tchadensis* (Brunet et al. 2002), as a taxon possibly related to the hominid stem species near the splitting of chimpanzee and hominid lines (Brunet et al. 2002; Wood 2002), may be supported by the estimation of life history dimensions that indicate an earlier evolutionary stage than all *Australopithecus* and *Homo* paleopopulations on the one hand and then the chimpanzee on the other. The Early Pleistocene (Upper Villafranchian) *Homo* paleopopulation of Dmanisi (Georgia) (*Homo georgicus*; Gabounia et al. 2002) has been interpreted as more closely related to the earliest Pleistocene *habilis* and *rudolfensis* than to the Later Early Pleistocene *ergaster* and *erectus* (Gabunia et al. 2000; Gabounia et al. 2002; Vekua et al. 2002). The life history estimates clearly support this view. The so-called *Homo floresiensis* (Brown et al. 2004) is not integrated here, as this specimen obviously neither represents a new species nor an enigmatic branch of hominid evolution, but is just a classic microcephalic *Homo sapiens* individual, sharing the characteristic syndrome of pygmy size, very small (chimpanzee sized) brain, and considerably aberrant skull allometries (Hemmer 1967). Perhaps this fossil may be interesting as an example of the survival of handicapped people in a Paleolithic culture. It may also help to understand the dysregulation leading to microcephalic development as a possible key to an intrinsic relationship of brain, maturation, and life history.

Conclusion

Relationships between the life cycle and body mass, brain mass, and relative brain size of extant primates can be used to estimate life history parameters of extinct species. Methods to predict the key variables body mass and brain mass from available cranial and postcranial materials of fossil hominoids, especially hominids, are compiled and evaluated. The final approach to life history data estimation in fossil hominoids, especially in fossil hominids, is a story of reliability of the prediction equations to be used. There is a wide variability in the results of body mass estimation obtained on the basis of different species samples used to create the equations, on the basis of different dimensions, and using different line-fitting techniques. The availability of several parts of a single skeleton allows for many independent estimates, which group together centrally to resemble a normal distribution, to give a clear and conclusive view of the most probable body mass of an individual and to allow easy recognition of outsider values and thereby of less useful predictor equations. The use of relative brain size instead of absolute brain mass or cranial capacity in life history correlations eliminates the influence of body size and allows for some further improvement of the correlation coefficient with most life history variables. Convincing estimates of corner stages of life history, the age at eruption of the first lower molar, the age at female sexual maturity, the age at first breeding, and the maximum life span, may be reached by this procedure. This is demonstrated for some key fossils, such data supporting their phylogenetic interpretation resulting from comparative morphological studies.

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Defining Hominidae
- ▶ Defining the Genus *Homo*
- ▶ Evolution of the Primate Brain
- ▶ Fossil Record of Miocene Hominoids
- ▶ General Principles of Evolutionary Morphology
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Modeling the Past: The Primatological Approach
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Primate Intelligence
- ▶ Primate Life Histories
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology

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Genetics and Paleoanthropology

Jonathan Marks

Contents

Abstract

The training and the nature of their data often lead geneticists and paleontologists to conceptualize evolution in different ways. This chapter looks at two basic evolutionary concepts – adaptation and phylogeny – and shows how scholars trained in those fields have utilized them differently. As the works of genetics and paleontology converge, notably with ancient DNA studies, we also find new complexities in homology, relatedness, and speciation.

Introduction

In 1917, the paleontologist William King Gregory framed the apparent conflict between genetics and paleontology in terms of two key issues: adaptation and phylogeny. Prominent geneticists, notably William Bateson and Thomas Hunt Morgan, had argued, first, that adaptation was a teleological mirage and, second,

J. Marks (✉)
Department of Anthropology, University of North Carolina, Charlotte, NC, USA
e-mail: jmarks@uncc.edu

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that phylogenetic inferences should take a back seat to genetic, mechanistic studies. Gregory, on the other hand, challenged his readers to doubt that cetaceans are adapted for swimming or horses for galloping – far from being a mirage, adaptation was a crucial aspect of evolution. Moreover, the talk of studying genetic processes before and instead of evolutionary products was not only crassly self-interested but intellectually pernicious: "…the time for developing phylogenetic conclusions and for revising comparative anatomy and classification is always *now*, as fast as the evidence can be gathered and analyzed" (Gregory 1917, p. 635).

Differing Views of Adaptation

The exchange between the anatomist and geneticists a century ago perhaps surprisingly is still resonant today, having been reframed by molecular biologists in the 1960s. Adaptation is the apparent fit between an organism and its environment. Aristotle believed it was the result of species simply having been built that way. Many centuries later, Darwin argued that it was rather the result of a long-term bias in the survival and reproduction of organisms that differed slightly from the average, in the direction of a better fit. In other words, adaptation is the result of history, rather than of miracle. Nevertheless, there was tension even in the first generation of evolutionary biology in the Victorian era. Herbert Spencer convinced Darwin that his phrase "survival of the fittest" was effectively synonymous with Darwin's own "natural selection." Darwin agreed, in *The Variation of Animals and Plants Under Domestication*: "This preservation, during the battle for life, of varieties which possess any advantage in structure, constitution, or instinct, I have called Natural Selection; and Mr. Herbert Spencer has well expressed the same idea by the Survival of the Fittest" (Darwin 1868, p. 6).

Yet there is a crucial difference between the two phrases. If only Spencer's "fittest" survive, then the descendant populations can be expected to be very fine-tuned to the environment, since they were not merely fitter, but fittest. The pores of the sieve, so to speak, would have been very small. Natural selection, on the other hand, makes no claim as to the relative size of the pores. Under extraordinary circumstances, only the fittest may survive, but it is primarily simply the fitter that survive. That necessarily implies a bit more tolerable unfitness between the organism and its environment than we might expect if only the fittest were surviving.

Through the mid-twentieth century, evolutionary theory had achieved a compromise whereby adaptation was generally seen as a result of the successive accumulation of beneficial genetic mutations (Fisher 1930). In parallel, the population geneticist Sewall Wright (1931) modeled how transient maladaptation might lead to even higher states of adaptation or how alternative states of adaptation could coexist, either from different combinations of alleles or from different alleles of equivalent survival value. This work influenced Dobzhansky's (1937, 1955) ideas that saw evolution as driven not so much by the fixation of superior alleles, but by the production of superior heterozygous genotypes, yielding populations in states of transient or stable polymorphism. Wright's work was also later developed by his student Motoo Kimura, who founded a Japanese school of population genetics, rooted in the study of genetic variations of equivalent selective value, or "neutral mutations" (Kimura 1968, 1983).

Concurrently, the earliest empirical studies of molecular genetic variation were showing that the detectable genetic differences between species were difficult to reconcile with a view of evolution that envisioned the sequential selection of slightly favorable mutations. For a notable example, human diabetes was found to be treatable by injections of insulin derived from a cow or pig pancreas, despite the fact that there are some structural differences among the hormone molecules. Far from being precisely attuned to cow physiology, the bovine insulin molecule works well in humans, which in turn seems to imply a great deal of "slop" in the genetic system. Discoveries such as these suggested empirically that the genetic study of evolution might best proceed in the absence of presuppositions about adaptation, that is to say, as "non-Darwinian evolution" (King and Jukes 1969).

The molecular biologist François Jacob (1977) famously argued that evolution acted not like an engineer, but like a tinkerer, drawing inspiration from the anthropologist Claude Lévi-Strauss's (1962) work on mythology. The storyteller, said Lévi-Strauss, does not compose an optimal story from scratch, but rather cobbles together available motifs and suitable themes and consequently relates a story that is familiar and resonant to its audience. In a similar fashion, argued Jacob, nature works with genetic systems that are passably functional, often redundant but, most of all, suboptimal, and transforms them into other novel systems with those properties. Thus, the metaphor of evolution as an engineer fails before the metaphor of evolution as *bricoleur*, or tinkerer.

This basic difference between the way geneticists and anatomists see adaptation is rooted in the nature of their subjects. Bodies are what adapt. They may do so genetically, over the course of many thousands of years. They also do so developmentally (and irreversibly): The body grows in certain characteristic ways in response to hypoxia or oxygen stress, for example. And they adapt as well physiologically (and reversibly), as in tanning or shivering or callousing under the stimulation of ultraviolet light or cold or abrasion. The point is that the fit between an organism and an environment is an ongoing, dynamic one (Lasker 1969). To survive is to adapt; consequently, if you study bodies, you are necessarily struck by the fit between what an organism looks like and how it lives. To study evolution, then, you are studying the transition from one adapted state to another; consequently, the anatomist focuses on the particular physical differences among species and explains them in terms of the adaptive differences between the species. The similarities require no explanation; one queries not the choice to remain on four legs, made by myriad primate species, but the change to two-legged locomotion. One does not query the retention of body hair in all other primates, but its reduction in one lineage. It is obviously good to be able to speak, but all the species that cannot speak seem to make do. The anatomist thus anticipates stability, which requires no explanation, and interrogates change, which does require an explanation, in terms of Darwinian directional selection.

A genetic comparison, however, works nearly the opposite way. The geneticist anticipates change (due to the constant fixation of new, nearly neutral mutations) and interrogates stability, for it implies constraints on the ubiquitous pressure to change. Consequently, when examining genomes of different species, we will expect to find differences, and we explain sequences that are "too similar" as being constrained by selection, because they are more functionally important than other sections of DNA, where differences are accumulating. This is precisely how the homeobox, a DNA regulatory sequence involved in the early development of the embryo, was discovered in the 1980s. How could anything in the DNA of flies and mice *not* be different (Gehring 1993)?

Consequently, where an anatomist can see adaptation, and inferentially the invisible hand of natural selection, a geneticist can see slop and wiggle room, produced by randomness and historical accident. The patterns they see, the questions they ask, and the explanations they invoke differ correspondingly. The geneticist sees a genome in which most DNA changes are neither good nor bad, mutation is a constant but light pressure on the integrity of the system, and most DNA sequences are consequently expected to change, indeed to degrade, with some degree of regularity. In fact, the regularity is so much of an expectation that the amount of detectable genetic difference between two species is generally taken not as an indication of how differently adapted they have become, but as a chronological meter of how long ago their gene pools separated. When we compare humans and chimpanzees genetically, for example, we see far more readily how similar their genomes are, not how behaviorally, ecologically, demographically, and cognitively different they are (Marks 2002). The DNA sequences of two animals that have recently become differently adapted are expected to be very similar, except for the constant pressure of mutation and for the very rare "really good" mutation that actually translates into a physical benefit. Consequently, if we study the human genome in a comparative context, we are more struck by what we do not see than we are by what we do see. We do not see the weight-bearing feet; there are no feet in the genome. Nor are there tans, nor shivers, nor callouses. There are genes there, not bodies, and it has proven remarkably difficult to match up human genes to human adaptations in any but a small handful of cases. Indeed, it is hard to find adaptation at all reliably in the genome (Graur and Li 2000; Graur et al. 2013).

We have known for a long time that although the DNA (or genotype) somehow encodes the body (or phenotype), the genetic elements do not correspond to the body parts in any simple way. This was known to an earlier generation as the "unit-character" problem (Castle 1930). Bodies adapt, because they actually interact with environments; and genomes do not, at least not directly. Moreover, the units of the genome do not map on to the units of the body. We have genes, units of hereditary instruction; and we have elbows, units of the arm – but we do not have "elbow genes." In fact, long after the completion of the Human Genome Project, we still know remarkably little about the production of a 4-dimensional (space-filling and maturing) body from a 1-dimensional set of instructions (the DNA sequence).

It is hard to overstate the implications of these divergent ways of approaching evolutionary data. Geneticists can see animals that look very similar, but whose genomes are scrambled – for example, gibbons and siamangs. Gibbon cells have 22 pairs of chromosomes, and siamang cells have 25. But that overstates their similarities, for most of the siamang chromosomes cannot even be identified in their gibbon counterparts, because so many rearrangements have arisen between them. (Homologous human and chimpanzee chromosomes, by contrast, can be readily matched up and identified almost perfectly.) Yet a gibbon sperm with 22 chromosomes can fertilize a siamang egg with 25 chromosomes and produce a living hybrid "siabon" (Myers and Shafer 1979). It is hard to avoid the conclusion that shuffling the genes around, while leaving them fairly intact, simply does not interrupt the production of gibbon bodies from their DNA sequences (Godfrey and Marks 1991). It is a system that cries of slop, not of precision.

The best-known cases of human genetic adaptations to environmental pressure are those to malaria, incorporating a range of blood diseases and other genetic variants, including sickle-cell anemia and thalassemia. But human populations more commonly have their own nonadaptive idiosyncrasies, notably elevated risks of other genetic diseases. These are accidental, not adaptive, for example, porphyria variegata among white Dutch South Africans, the genetic legacy of a seventeenth-century settler (Dean 1971).

Along the lines of sickle-cell anemia, the prevalence of Tay-Sachs disease in the gene pool of Ashkenazi Jews has been suggested to be a genetic adaptation. Carriers, in this framework, have been suggested to be more resistant to tuberculosis (Myrianthopoulos and Aronson 1966) or a bit smarter than noncarriers (Cochran et al. 2006). Nevertheless, it is unclear from the population genetics whether selection has operated at all, with over 80 % of the Tay-Sachs alleles in Ashkenazi Jews being identical, suggestive of a strong "founder effect" (Frisch et al. 2004). Indeed, the higher prevalence of the disease in French Canadians and Cajuns is interpreted in precisely this way. Cystic fibrosis, more common in northern Europeans than in other populations, has been associated with resistance to many different diseases, all plausible, but none established (Valles 2010). While the existence of many alleles causing cystic fibrosis is consistent with an inference of selection, the preponderance of a single one – ΔF508, comprising locally between 40 % and 80 % of the CF alleles in Europe – suggests the complex interplay of stochastic and deterministic forces (Bobadilla et al. 2002).

The point is that we ought to be able to distinguish between these alternative explanations, selection (leading to adaptation) or drift (leading to nonadaptation). But usually, even with the finest-grained genetic data, we cannot. Usually the best we can do is to show that some feature of the genome is more uniform and less divergent than we think it ought to be, and speculate about the reason that its patterns of difference might be so unexpected. This is based on mathematical algorithms that often produce high proportions of false-positive results, however.

In some cases, DNA sequences that are too different can be identified, but the adaptive story behind them may be thin and insubstantial. The gene called FOXP2 impairs cognitive linguistic competence when mutated. Three coding-sequence mutations differentiate the human gene from the mouse gene, two of which occurred recently in human evolution, because even the chimpanzee lacks them.

It is certainly a gene involved in language, but is it a language gene? After all, rhesus monkeys and chimpanzees have the same coding sequence, but have quite different vocalizations and cognitive properties. The orangutan has a unique coding-sequence mutation, but no obvious special communicative faculties. And one of the unique human mutations arose in parallel in Carnivora (Enard et al. 2002; Fisher and Scharff 2009). So one can make a strong case for this gene being nebulously "involved" in cognitive linguistic function, but a considerably weaker case for this gene to be a selectively driven master human language gene, as it has often been represented. The problem is that selection occurs on phenotypes, and genotypic data are difficult to translate phenotypically; to think of FOXP2 as a master language gene is to fall into the trap of unit characters.

Students of human evolution have repeatedly pointed out that it is unwise to assume that any particular feature is an adaptation, specifically arisen by natural selection, regardless of how useful it seems today, in the absence of strong supporting evidence (Hooton 1930; Washburn 1963; Gould and Lewontin 1979). Use does not explain origin, since any trait may have multiple uses, which may assume different degrees of importance in particular contexts. This is readily visible in cultural evolution, where (despite the limitations of the analogy to organic evolution) origins are often known and can easily be shown to be different from later primary uses – for example, gunpowder for entertainment and the Internet as a means of decentralizing computers in the event of nuclear attack. The features indeed found new uses, but to attempt to infer their origins from their predominant modern uses would be highly misleading.

Many centuries ago, Aristotle explained adaptation by reference to a saw (Ogle 1882). A saw is made for a particular reason, to cut wood, and that reason is its purpose for existence. It would be ridiculous to imagine making a saw, trying to figure out what to do with it, and then serendipitously discovering that it was useful for cutting wood. But Aristotle's saw was a carefully chosen cultural feature. If he had chosen something as mundane as clothing, whose purposes include warmth, concealing taboo body parts, aesthetics, physical protection, comfort, and the communication of a social identity, his error would have been obvious. Old features have multiple uses; some of them may be new and they may affect our perception of what the feature is primarily used for, which may be quite different from how it got started. The point is that living organisms can be surprisingly good at making do with what they have. We know of ways that adaptive, nonadaptive, and even maladaptive features can evolve genetically. The choice of whether to see crafted machinery in nature, or *bricolage*, that is to say, genetic elements cobbled together into a stable functional state, as modern molecular geneticists do, is neither right nor wrong. They are divergent approaches that can both be reconciled to evidences of the history of life.

We can study what a feature does, and we can study how it got there, but to ask what it is *for* is to decorate the scientific question with metaphysical accessories. To ask what it is for is to assume that there is a reason for it – a deterministic narrative incorporating a selective regime for the feature and a particular optimal solution to a problem. But actually, there may be no reasons for some things, just naturalistic causes and uses, and much random noise; life may be more like clothes than like saws.

Genetics and Phylogeny

Gregory's (1917) other conflict between genetics and paleontology concerned prioritizing evolutionary processes, which geneticists studied, over evolutionary products and patterns, which anatomists studied. In fact, however, biochemical research was already proceeding on issues of systematics and phylogeny. The study of animal relations by the study of their blood reactions was known as "systematic serology," pioneered by G. H. F. Nuttall (1902, 1904). In the context of comparing serological reactions among many vertebrate species, Nuttall found that lemur blood did not react discernibly with human and suggested that lemurs might not really be primates. This conclusion was dismissed by the anatomist Solly Zuckerman (1933), but defended by the serologist Alan Boyden (1942). So what had actually failed – the lemurs or the test? Zuckerman found that tarsiers failed the blood reaction test too, and since they are more obviously primates than lemurs are, it stood to reason that the test was a failure, not the prosimians.

Systematic serology did yield an interesting result, however. According to the work of Christian von Krogh (1937), human and chimpanzee blood seemed more similar to one another than either was to orangutan blood, as had indeed been articulated even earlier by Guyer (1925). This conclusion was reiterated in the most popular mid-century text of physical anthropology: "The weak similarity of the orang to other species suggests a lengthy process of separate development for this animal and its early branching off from the stock of chimpanzee and man" (Hooton 1946, p. 45). When the claim was rearticulated by Morris Goodman a generation later (1963), it came with a call to reclassify the apes on phylogenetic grounds. This claim was roundly rejected, however, as zoological classifications were built from the negotiation between ancestry and adaptation (Gregory 1910; Simpson 1945, 1961; Mayr 1969). Even more senior systematic serologists found the claim more brash than insightful (Hagen 2009). To construct a classification solely based on ancestry was not considered to be a scientifically valuable enterprise, until the popularity of cladistics some years later.

In the mid-1960s Allan Wilson and Vincent Sarich, following on the suggestion by Zuckerkandl and Pauling (1965), were able to quantify the data of systematic serology and found that the amount of serological difference between two species, which was an estimate of the genetic difference, appeared to be related simply to the time since the two species diverged, not related to any adaptive differences between them. In other words, the "immunological distance" between an orangutan and a baboon was very similar to the distance between a human and a baboon, reflecting the time since a common ancestor of human and orangutan diverged from the baboon, and *not* reflecting the fact that humans are brainy, fatty, cooperative, hairless, sweaty, and bipedal. When applied to the divergence of human and chimpanzee, the two species appeared to have separated rather less than 5 million years ago, much more recently than the fossil record seemed to suggest (Sarich and Wilson 1967a, b). The fossil evidence had been over-interpreted, and the two conclusions of Sarich and Wilson have held up remarkably well. Molecular evolution does proceed in a "clocklike" fashion, and the relationships between humans and the African apes are sufficiently close as to suggest that they diverged from one another only in the latest Miocene, perhaps 6–8 million years ago.

This argument was built upon temporal inferences, not directly upon phylogenetic inferences. With the advent of protein and later DNA data, it became possible to reconstruct species divergences from cellular or genetic information, just as one might use dental or anatomical information. The two manners of utilizing these data mirrored the ways that biologists generally were considering phylogeny, using quantitative distance methods in the 1970s (Sokal and Sneath 1963) and qualitative trait distributions in the 1980s (Eldredge and Cracraft 1980) and later combining them.

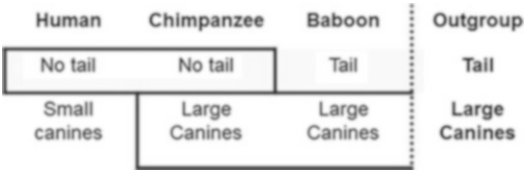
However, it is not the case that molecular-based inferences are necessarily more reliable than anatomically based phylogenies. Genomes and bodies do not map on to one another well, as previously noted, and their evolution, while tracking the same history, nevertheless involves different processes and inferential methods. Organisms cannot be epistemologically reduced to their genomes (despite the old hype on behalf of the Human Genome Project). To use a crude example, the chemistry of DNA statistically compels your genome to match that of a cantaloupe, on the average, once in every four sites randomly, since a DNA sequence is composed of only four bases. Thus, the same DNA sequence measurement that may seem so overwhelming when applied to the chimpanzee (over 98 % base-for-base match to a human) seems underwhelming when applied to the cantaloupe (about 25 % base-for-base match). There is, after all, no significant biological sense in which you could reasonably consider yourself to be one-quarter cantaloupe – except by DNA comparison!

The patterns of human evolution as recorded and analyzed in the genes and as recorded and analyzed in the body obviously have to be similar, since they are recording the same events of biological history. Ideally, genetic and anatomical data ought to provide independent tests of phylogenetic hypotheses; in practice, however, the testing is often one sided. As early as 1964, the paleontologist George Gaylord Simpson identified the problem as "semicircular reasoning": "[A]greement between the two has been taken as the requisite validation of the molecular approach to phylogeny, but nonagreement has been taken as evidence of the greater reliability of the molecular method" (Simpson 1964, p. 1535).

The problem is not that one is better than the other; it is that they each have their own sets of assumptions and methods, and when their products don't match, they both have to bear close scrutiny.

Distance methods have the advantage of being able to incorporate large classes of data, but they reveal patterns of similarity and difference, not evolutionary divergences, and can only be related to evolutionary divergences when assumptions are made about the rates and modes of change. Cladistic methods work by taking two character states distributed across three taxa (say, tail/no-tail

Fig. 1 Distribution of two characters, each with two character states, across three catarrhine taxa and a platyrrhine outgroup



or large canines/small canines across baboons, chimpanzees, and humans) and asking which two of the three taxa are likely to be closest relatives, on the basis of that distribution. By establishing the ancestral condition in an outgroup (large canines and tail in a platyrrhine monkey), it follows that evolution proceeded away from that condition, and thus the relevant changes involved losing the tail in an ancestor of humans and chimps and reducing the canines in an ancestor of humans. Thus, sharing "no-tail" links humans and chimps as close relatives, for the tail was lost in a common ancestor of human and chimp; but sharing "large canines" does *not* link baboon and chimp as close relatives, for the evolutionary event that occurred among the three taxa under consideration was reduction of the canines in the human lineage (Fig. 1). Sharing large canine teeth simply marks two of many lineages in which an evolutionary change did not occur.

We can draw those inferences because our assumption holds that levels of homoplasy (parallel acquisition) are low relative to synapomorphy (sharing features by virtue of recent common ancestry). So if "having four limbs" arose independently in lizards, cows, baboons, and people, or if hairy skin arose independently in cows, baboons, and people, there would be a problem in deriving those animals from a single, unique four-legged ancestor or hairy ancestor, respectively. But it does seem, given the anatomical and fossil data, that growing four limbs or body hair is a sufficiently rare occurrence that it is a good marker of common ancestry and unlikely to have emerged independently in more than one of the lineages in question.

On the other hand, the possession of, say, a G at a random place in the genome is not quite such a rare event. Not only is mutation a constant pressure on the genome, but there are only three things for a G to mutate to (A, T, or C, although more likely A, because it is about the same molecular size as G). What that means is that the theory behind phylogenetic reconstruction necessarily has to be a bit different for DNA sequences than it is for body parts. Generally, that entails quantifying the amount of genomic differences (since there may be millions of them in a genomic comparison) and deciding that the tree that takes the smallest number of inferred mutational changes – the most "parsimonious" tree – is the best tree, that is to say, the one that most accurately encodes the history of the species.

There are important, often uninterrogated, assumptions that go into such comparisons. Often these create problems for understanding homology in the genome, which may be far more problematic that it is anatomically (Thornton and DeSalle 2000).

In addition to nucleotide substitutions, which are most amenable to quantitative treatment, there are insertions and deletions (indels), which are rarer, as well as movable elements, variable number of tandem repeats (VNTRs), and cellular mutational processes by which one DNA sequence can be used as a template to "correct" the DNA sequence adjacent to it. It is not uncommon to find, for example, that a sequence of AAA might be homologous to a sequence of AAAAAAA in another species. Does this represent five one-base indels or one five-base indel? The question is consequential to the extent that one is fundamentally attempting to establish the amount of genetic change that has occurred between the two species in question.

This becomes more problematic with more distant comparisons. The molecular evolutionist is trying to infer the number of evolutionary changes that have occurred from the number of evolutionary differences that are observable. Observing an A in one species and a G in another may lead to the inference of a single mutation having occurred (say, A to G), but there is a small probability that it actually represents two mutations: A to C and then to G. The more distant the relations, or the more rapidly the particular bit of DNA evolves, the greater the likelihood that the number of observed differences underestimates the actual number of evolutionary changes. By making certain assumptions about the rates and modes of evolution, one can computationally adjust for the discrepancy, but this introduces the problem of a gap between observations and evolutionary inferences. There are several ways of correcting that mathematically, but they leave large uncertainties in the phylogenetic results. The problem is an inherent contradiction in the reasoning: One is choosing the most parsimonious solution in a system that is intrinsically unparsimonious. Statistics can never fully compensate for problematic epistemology. Indeed, this can lead to absurdities, such as "the [genomic] difference between galago and human . . . is about 170 %" (Doan 2003), as if two entities could reasonably be judged as 170 % different from one another. Rather, it means that one is inferring two mutations to have occurred, one of which is invisible, nearly every time one sees a single difference between the two DNA sequences.

Other genetic traits, such as the presence or absence of mobile particular genetic elements, may be more useful for cladistic inferences (Xing et al. 2007). In practice, most of the time phylogenetic trees derived from DNA are concordant with those derived from anatomy. But, as Simpson (1964) queried, in the rare cases where they do not concord, how do we know which tree to trust? For example, some genetic studies locate the proboscideans (including elephants) as especially closely related to the carnivores and artiodactyls, among the mammals. Most other analyses place the elephants as no closer to the dogs and cows than are rodents or monkeys (Dolgin 2012). What to believe? In short, we are obliged to view any analysis of genetic data as valuable, but accompanied by its own set of methodological limitations, and sometimes yielding incorrect inferences (Penny 2013). Where genetic analysis had once suggested a very ancient divergence for the modern mammalian orders (Hedges et al. 1996), that inference is now roundly rejected (O'Leary et al. 2013).

Where genetic data once revealed human races (Boyd 1963), now they do not (Madrigal and Barbujani 2007).

Fossil DNA

A suite of osteological traits is used to diagnose Neanderthals and to distinguish them from anatomically modern humans. As anyone who teaches undergraduates can attest, these features are sufficiently subtle that they need to be carefully pointed out to students, for they are actually obvious only to specialists. When genomics researchers were able to sequence the DNA from Neanderthals, they reinforced the conclusion that Neanderthals were subtly, yet distinctively and diagnosably, different from modern humans. Shortly thereafter, geneticists sequenced the DNA from a 50,000-year-old finger bone found in a Siberian cave. The DNA from this site, called Denisova, has yielded several odd results. First, the mitochondrial DNA (mtDNA) seemed to suggest that it was distinct from both human and Neanderthal DNA (Krause et al. 2010). Second, the nuclear or genomic DNA seemed to show it to be a divergent variant of Neanderthal DNA (Reich et al. 2010). Third, the Denisovan genomic DNA seems to have more similarity to the DNA of modern Oceanic peoples, such as New Guineans, than to other modern humans, including Siberians (Reich et al. 2011). And fourth, the DNA from a toe bone in the same stratum is more like the DNA of Neanderthals than like the finger bone (Prüfer et al. 2014).

These results are highly paradoxical and are difficult to make sense of, particularly the geographical problem of imagining Middle Pleistocene Siberians to stand in a special relation of ancestry or kinship to Melanesians of today (Hawks 2013). To make sense of these data, we have to bear in mind that Neanderthals are defined anatomically, but Denisovans are only known genetically (two teeth and a toe bone have since been discovered at the same site, none diagnostic), and their relationship to one another is obscure at best. Based solely on the Denisova sample, it is certainly a reification to imagine a population of "Denisovans" stretching across Asia. Further, the human gene pool is notably depauperate in genetic diversity, being perhaps 5–10× less variable than the gene pools of chimpanzees and gorillas, who are, of course, far less numerous and far less geographically cosmopolitan than humans are (Kaessmann et al. 2001). We do not know precisely how or when our ancestors became so genetically homogeneous, or the nature of the "lost" genetic diversity, or even how that fact might affect the interpretation of these comparisons. Finally, the special genetic similarity of modern humans to 50,000-year-old Siberians may be illusory, since mathematical models have indicated that, in relation to the present human population, the ancestral human gene pool demographically collapses by about 10,000 years ago (Rohde et al. 2004). In other words, anyone alive 10,000 years ago was a common ancestor of all living people or of no living people. The meaning of shared DNA segments between particular modern populations and Siberians of 50,000 years ago would thus be unclear and certainly far removed from ordinary notions of descent and relatedness.

Trees and Rhizomes

The cultural aspects of ancestry, even in evolution, emerge in interesting ways. Since the cessation of gene flow classically implies a new species and a new evolving lineage, it has traditionally been assumed that, above species level, gene pools can only diverge from one another, since they can't get more similar through gene flow or interbreeding. Consequently the most famous image of evolution is as a tree, its branches ever diverging from one another. This produces our classical scientific notions of descent and relatedness, which are those being applied to the relations of Neanderthals, humans, and "Denisovans" with such curious results.

That is an image for macroevolution, however. For microevolution, we must look to another part of the tree – to its root system. Roots, unlike branches, are not always separating from one another. Roots may often fuse with one another and create a connected network whose individual branches may be very difficult to delineate (Arnold 2008). They are like populations of organisms, evolving somewhat separately, but connected by gene flow, and never entirely distinct. Tree-building algorithms may be inadequate to the task of reconstructing relatedness among entities that not are related to one another as branches of a tree (Templeton 1998).

Likewise, the genetic relationships among humans, chimpanzees, and gorillas were known by the 1980s to be (a) very close and (b) phylogenetically ambiguous. To the extent that a pairwise "resolution" of the three-way divergence could be established, it invariably was accompanied by a high degree of uncertainty. Consequently, the relations among the three living genera were often rendered as a three-way split, or "trichotomy." The introduction of DNA sequence analysis finds the human and chimpanzee to be consistently closer than either is to the gorilla, but with a high amount of discordant data (Chen and Li 2001). These are generally interpreted to be the results of (1) parallel mutation (Goidts et al. 2005; Marques-Bonet et al. 2009); (2) complex segregation of ancestral polymorphisms, or incomplete lineage sorting (Prüfer et al. 2012); and (3) backcrossing or trans-specific hybridization (Patterson et al. 2006). Significantly, however, although it can be rendered compatible, this tree is discordant from the tree one would derive from solely anatomical evidence (e.g., Collard and Wood 2000).

Rather than trying to explain away a large amount of discordance, it may be more useful to reconsider the underlying evolutionary model. The paleontological view of speciation that is most compatible with cladistics and punctuated equilibria sees speciation occurring at a geological instant, as an "event." But a consideration of reproductive and population genetics necessitates seeing speciation as a "process."

Another wrinkle in tree making is the fact that anatomies are canalized, that is to say, they are generally uniform in spite of underlying genetic variation. But the underlying genetic variation is there, and may be more difficult to sort, if one looks at the DNA rather than at the body, because there is so much DNA. For example, we find that mammals have hairy skin; we don't find polymorphism, such that some mammals have hairy skin and others have feathers. On the other hand, polymorphism is far more common for genetic characters (A, G, C, and T), and some of it gets sorted into descendant lineages in discordant ways. How much? That depends on the specific genetic regions, the demographic histories of the species, and the genetic structure of the extinct ancestors, which may be simply unknowable.

Here is a relevant, simple scenario for the early ancestry of humans. Suppose an ancient, late Miocene chimpanzee-like population of animals, widely distributed across central Africa, gave rise to a group of gorilla-like creatures in the western part of its range and, around the same time, to a group of humanlike creatures in the eastern part of its range. Then the humanlike creatures expanded their numbers at the expense of the gorilla-like and the remaining chimp-like creatures. Then a few million years later, one tries to compare the genomes of one or two specimens of each and demands to know which two of the three species are the closest relatives. One would probably find a lot of phylogenetic discordance, many features that appear to link humans to the ancestral proto-chimps, and many features that appear to link gorillas to the ancestral proto-chimps. One probably would not find much that appears to link humans specifically to gorillas, because they would not stand in an especially intimate phylogenetic relationship to one another.

And although one could force all three genera into a mold that shows them as having experienced two consecutive binary splits, that would not reflect the actual demographic and phylogenetic history – it would be simply imposing a historical model upon the data, rather than extracting it.

And that is indeed essentially what one finds. Chimpanzees are closely related to humans and also closely related to gorillas, although that latter fact has tended to get lost in simplistic renderings of our phylogenetic history. One recent high-tech genomic study was so committed to binary splits that it depicted gorillas “splitting” at 5.95 million years ago, and then chimps and humans “splitting” from one another at 3.7 million years ago – but also imagined a strain of gorillas returning to sodomize their chimpanzee cousins (Scally et al. 2012). The reason for this creative phylogenetic scenario is that fully 30 % of the DNA sites that could be used to link two of the three genera actually linked the “wrong” two – that is to say, they linked chimpanzees to gorillas, rather than to humans. This is only a problem, though, if one is constrained by the bifurcating tree as a metaphor for the evolution of species. If, instead, we conceive of speciation as a process (rather than as an event), of population differentiation as a microevolutionary demographic phenomenon, and of the bifurcating tree as an inapplicable metaphor, we might come closer to the actual history that is embedded in the genetic data. That history would be one of populations becoming differentiated, but incompletely separated, and significantly long periods of gene flow, without an actual pair of closest relatives and lots of “wrong” data (Fig. 2).

A three-way split or more, in a fragmented habitat, over a short span of geological time, might describe late African ape evolution more accurately. That may be a major source of phylogenetic ambiguity: In other words, trying to force evolution into dichotomous molds, to make bifurcating trees, may be a variant of the old square-peg/round-hole problem (Fig. 3).

Fig. 2 Divergences of human, chimpanzee, and gorilla, with trans-specific introgression, after Scally et al. (2012)

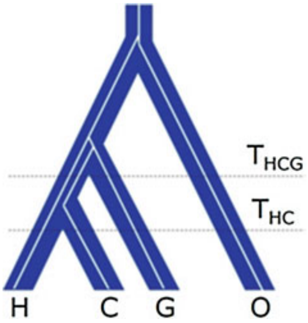
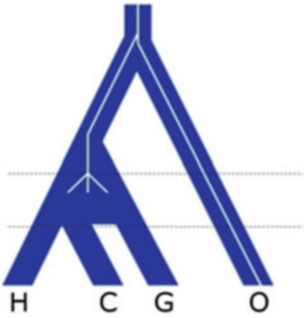


Fig. 3 Relations of human, chimpanzee, and gorilla depicted as incomplete speciation over a significant period of time, incorporating geographic, demographic, and population genetic complexity



The tree metaphor is of course broadly applicable in understanding the history of life, as Darwin and Haeckel appreciated, but it is breaking down in diverse areas. We now know there to be horizontal exchanges of genetic information between species, with viruses as vectors. Near the root of the tree of life – that is to say, as we try to reconstruct the origin of life and its primary "branches" – it turns out that the branches emerge not from a trunk, but from a web. That is probably because life emerged before species did, and the tree metaphor only really applies to well-formed species.

Consequently, below the species level, the phylogenetic issues are much more vexing. The species that most directly concerns us, *Homo sapiens*, has many formal divisions, but they are culturally based; and it has biological diversity that does not sort us into meaningful natural divisions. The categories "French" or "Latino" or "Lutheran" are meaningful without being natural or biological; and the categories "albino" or "over 6′3″ tall" or "toddler" are natural while only being narrowly meaningful.

One could certainly ask whether the French are genetically more closely related to the English or the Swiss, but of course since those are political categories, the answer one gets will depend crucially on who represents the French, the English, and the Swiss in the study. So it is a foolish question, rather like asking whether architects are genetically more closely related to doctors or to air traffic controllers. The concept of relatedness is here consequently a biocultural concept, not a strictly natural one, because the categories of people being compared are not natural categories of people.

While once again, computers can be programmed to deliver bifurcating trees of human populations based on their genes, as geneticists armed with computers have realized since the 1960s. There are two problems with this. First, one does not need a computer or a geneticist to determine that a Swede and a Dane are more closely related to one another than either is to a Navajo. People from nearby are invariably more similar and more closely related than people from far away. And second, gene flow – the horizontal contact between populations that accompanies their vertical descent – means that the image that most accurately represents the metaphoric structure of the human species is the rhizome or trellis or capillary system (Wolpoff and Caspari 2000). In other words, closely related peoples are not really representable in a treelike fashion, because they have never really diverged, even though they may be statistically slightly different from one another. The classic physical anthropologists of the mid-twentieth century knew that and struggled with representing it (Hooton 1946).

Today, geneticists still sometimes reduce human population histories to a series of splits, as their computer programs often require that simplistic assumption. The interesting question, though, is not whether "for example, the Irish are more closely related to the Spaniards or to the Swedes" (as a respected population genetics website naively queries –http://hsblogs.stanford.edu/morrison/2011/03/10/human-genome-diversity-project-frequently-asked-questions/, accessed 10 October 2013), but rather how to conceptualize and represent the relationships among human populations as microevolutionary, not macroevolutionary and treelike.

Conclusion

Scholars trained in genetics and in anatomy often see evolutionary comparisons in quite different ways. They may differ in the ways that they invoke adaptation, natural selection, and speciation. In fact, even with the finest-grained genetic data, it may be difficult to distinguish the "invisible hand" of selection from the stochasticity of genetic drift. Genetics nevertheless carries a great deal of cultural authority, particularly in the wake of the Human Genome Project, so it is easy to overlook the limitations of genetic comparisons, particularly when the limitations of the fossil record are so familiar. History shows, however, that there are always learning curves and missteps in the application of genetic technologies to questions of human evolution. Anatomical and genetic techniques each have their own set of strengths and weaknesses, which may need to be carefully evaluated when they produce apparently discordant results. One of the more difficult issues in contemporaryevolutionary theory involves the imposition of a dendritic, or treelike, model upon evolutionary histories that may be more complex, thus concealing that complexity.

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Cross-References

- ▶ Ancient DNA
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Neanderthals and Their Contemporaries
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Quantitative Approaches to Phylogenetics
- ▶ Species Concepts and Speciation: Facts and Fantasies

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Ancient DNA

Susanne Hummel

Contents

Abstract

Ancient DNA research, defined as the retrieval and analysis of DNA sequences from various degraded biological source materials, has promoted many biological and medical research fields during the last three decades. In particular, historical anthropology and paleoanthropology stand to benefit from direct access to back-dating genetic data, as has already been shown through

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S. Hummel (✉)
Institut für Zoologie und Anthropologie, Historische Anthropologie und Humanökologie,
Georg-August-Universität Göttingen, Göttingen, Germany
e-mail: shummel1@gwdg.de

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applications ranging from individual identification to reconstruction of kinship and marriage patterns to human phylogeny. The DNA-based prerequisites and basic methodological strategies for access to the various types of information are explained, as well as the characteristics of ancient DNA that limit the different approaches. Major restrictions arise from the degradation of ancient DNA down to fragment sizes of only a few hundred base pairs or less. This fact links ancient DNA analysis to either the PCR technique or to Next Generation Sequencing (NGS) approaches, both of which make it possible to deduce genetic information from degraded nucleic acids. Futhermore, ancient DNA extracts regularly consist of only a few intact target sequences, which may harbor sequence deviations due to the degradation process. Both these factors make the analysis vulnerable to the generation of non-authentic results. These pitfalls of ancient DNA analysis are explained and discussed in detail, with reference to the most recent relevant literature. Wherever available, suggestions for strategies to overcome commonly experienced obstacles in ancient DNA analysis are highlighted and evaluated.

Introduction

Today, the analysis of ancient degraded DNA, extracted from forensic evidence samples and archaeological specimens hundreds and thousands of years old, is common practice. It was the coincidence of two events, three decades ago, that enabled this remarkable and comparatively rapid development. On the one hand, there were the first reports on the retrieval of ancient DNA from a specimen of an extinct quagga more than 100 years old (Higuchi et al. 1984) and a specimen of an Egyptian mummy 2,400 years old (Pääbo 1984) that electrified many scholars working on historic and prehistoric biological sample materials. On the other hand, PCR was invented, enabling the enzymatic amplification of short specific DNA sequences (Saiki et al. 1985), which proved to be a true breakthrough to a new level of information for any biological and medical discipline. Only through the PCR technique did ancient DNA research, defined as the retrieval and analysis of degraded DNA sequences from forensic evidence, museum specimens, archaeological finds, fossil remains, and any other degraded traces of DNA, become viable.

In the context of population genetics, it is generally possible with the help of model calculations to deduce former states from present day genetic patterns (Barbujani and Bertorelle 2001; Cann 2001). However, these approaches may suffer from heuristic assumptions that fail to prove their applicability. Biases may be caused by, e.g., unknown bottleneck situations, unknown selective forces, or the unreliability of the molecular clock model. Therefore, direct access to historic and prehistoric genetic patterns has been a desideratum ever since ancient mitochondrial and nuclear DNA (nDNA) proved to be approachable through PCR (Hagelberg et al. 1989; Hummel and Herrmann 1991; Jeffreys et al. 1992; Gill et al. 1994).

In the early days of ancient DNA research, the common aspect for scholars from different scientific backgrounds was the fact that their investigations dealt with a demanding sample material (Herrmann and Hummel 1993). However, within a short time, the field has diversified, and thousands of manuscripts that can claim to be ancient DNA research work have now been published. Among the various scientific contexts are, for example, epidemiology and public health (for reviews see, e.g., Zink et al. 2002; Greenblatt et al. 2003; Drancourt and Raoult 2005), nutritional sciences and food technology (Miraglia et al. 2004; Kato et al. 2005; Teletchea et al. 2005), histopathology and laboratory medicine (Leiva et al. 2003; Mariappan et al. 2005; Paik et al. 2005), forensic sciences (Iwamura et al. 2004; Valenstein and Sirota 2004; Budowle et al. 2005; Carracedo and Sanchez-Diz 2005; Sipoli Marques et al. 2005; Tamaki and Jeffreys 2005), human evolution (Cavalli-Sforza and Feldman 2003; Kaessmann and Pääbo 2004), paleobotany (Gugerli et al. 2005), and historical anthropology (Keyser-Tracqui et al. 2003; Hummel 2003a, Haak et al. 2008). Although the underlying scientific questions have significantly diversified since the beginning of the new millennium, a common theme for discussion remains, namely, the question of the authenticity of ancient DNA results. This discussion was prompted by a list of criteria (Cooper and Poinar 2000) which – according to the authors – ought to be adhered to in any ancient DNA analysis. However, it was obvious that these criteria concerned themselves only with rather general types of difficulties encountered in the analysis of ancient mitochondrial DNA (mtDNA), in particular where only few or single specimens were available, and should be replaced by a sensible experimental design focused on the actual concerns of each individual investigation (Hummel 2003a, b, Gilbert et al. 2005, Bandelt 2005).

At present this long-lasting debate has fallen silent, which is most likely owed to the fact that new technologies involving whole genome sequencing entered the scientific scene a few years ago – technologies which rapidly turned out to be particularly promising for all kinds of evolutionary biology questions (for reviews see, e.g., Huynen et al. 2012, Rizzi et al. 2012, Disotell 2012). In the case of hominid evolution, this means that the effort to answer questions concerning the co-existence of Neanderthals and anatomically modern *Homo sapiens* from comparatively short parts of the mitochondrial genome (Krings et al. 1997, 2000; Ovchinnikov et al. 2000; Caramelli et al. 2003, 2006; Beauval et al. 2005; Lalueza-Fox et al. 2006; Orlando et al. 2006), which earlier had to be PCR-based, will soon be on firmer ground. This will be achieved as soon as complete genomes of Neanderthals (Green et al. 2010), Denisovan (Krause et al. 2010a), and anatomically modern human individuals (Krause et al. 2010b) have become more numerous. Some caution is called for, however: the initial studies of the so-called Neanderthal genome project (Green et al. 2006, Noonan et al. 2006) were soon controversial, since they revealed inconsistencies most likely due to modern human DNA contamination (Wall and Kim 2007). This case demonstrated that a contamination hazard exists whenever the species under investigation is close to or identical to the investigators. Next Generation Sequencing (NGS) technologies are designed not to exponentially amplify short fragments but to sequence the extracted DNA sequences, but this does not eliminate the hazard. Therefore, independent of whether PCR or NGS technologies are being employed, experimenters must take care to adhere to the basic guidelines for contamination prevention during all steps of DNA sample preparation. Beyond that, it seems of course reasonable to adapt the experimental design as closely as possible to the scientific question at hand.

Ancient DNA Sources and Characteristics

Genetic information may be preserved in any type of biomaterial which at some point contained cells. In the average animal cell, basically the entire genetic information characterizing the respective individual is coded in the diploid set of chromosomes and hundreds to thousands of mitochondrial genomes. In plants, the chloroplasts also contribute to the genomic information. However, already in the living organism, cell organelles may suffer from normal processes of partial or complete degradation e.g., the decline of the nucleus in keratinous cells of hair and nails during growth. And whereas in plants, seeds are already designed by nature to preserve genetic information through time, a similar situation is not given in animals. However, even in animals, skeletal materials – such as bone and teeth – harbor cells in a more or less intact state of preservation through the ages. Within those tissues that are characterized by a high content of inorganic material and by high density, several different cell types are DNA sources: osteoblasts, osteoclasts, and osteocytes, which are responsible for bone remodeling and homeostasis, as well as all types of blood cells found in the Haversian canals. Aside from the cells representing the genotype of the organism whose skeletal remains were found, cells of pathogens that at some point entered the blood stream may also be preserved.

Typically, the majority of ancient DNA is degraded down to fragments smaller than 200 base pairs (bp) in length. This can reproducibly be shown through multiplex approaches (Fig. 1) which simultaneously amplify DNA fragments of different lengths ranging from 100 to 350 bp.

The typical signal patterns observable in electropherograms of multiplex amplifications indicate comparatively high yields of DNA fragments smaller than 200 bp and lesser yields of larger fragments. These patterns are not dependent on possibly varying amplification efficiencies of the different primers, or preferential amplification of shorter fragments, but entirely reflect the relative amounts of the target sequences. This should be considered when choosing and optimizing PCR parameters.

DNA Degradation

Whether the genetic information of an organism will be preserved just for days and weeks or for hundreds and thousands of years depends on many chemical and biological factors; these factors are interconnected in a highly complex manner and are, therefore, hardly understood and almost impossible to predict. In light of the cumulative empirical findings of many researchers and a small number of systematic studies (Burger et al. 1999; Caputo et al. 2011), certain factors favoring the

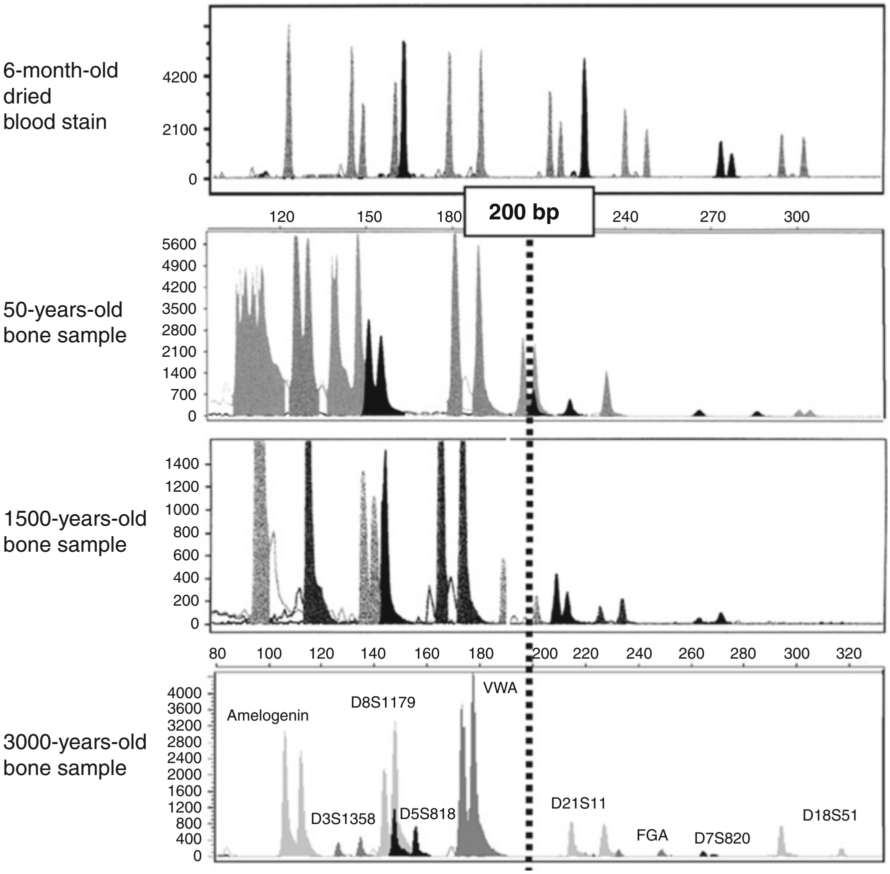


Fig. 1 Electropherograms of 40-cycle STR multiplex amplifications reveal characteristic differences in signal intensities depending on the length of the amplified fragment. The peaks reflect the typical degradation patterns of ancient DNA. While such pattern is only weakly present in 6-month-old dried blood stains, analyses of forensic and archaeological bone specimens reveal the patterns clearly. For the choice of amplification parameters, it may therefore be recommendable to work with varying cycle numbers, in order to enable proper detection and allele determination of amplification products of different lengths

preservation of partly intact DNA seem undisputedly clear: low temperatures and the absence of humidity, accompanied by a neutral or slightly basic pH value. In general, however, only very few studies have investigated the link between characteristics of the sample material and DNA preservation (Ottoni et al. 2009; Sosa et al. 2013).

Immediately after death, favorable conditions are best realized in bones and teeth, due to their high mineral content. When the environment of the decomposing body provides an optimal situation for preservation, the enzymatically driven autolytic decay is soon stopped; at the same time, the subsequent decomposition of remaining tissues through microfauna, bacteria, and fungi is less likely to take place effectively. The result is a mummification of the cells which, once it has occurred, may well last for thousands of years. The DNA within the mummified cells is now protected from the initial, main destructive processes: hydrolysis and the activity of exonucleases and endonucleases. The DNA will still suffer from a certain amount of destruction (e.g., oxidative damage), but much less so than in the course of early decay.

As a matter of fact, the mere preservation of macromorphologically intact skeletal material indicates pH values also favoring DNA preservation. If prehistoric pH values had been as acidic as was claimed in a paper (Lindahl 1993) that was often cited in the context of DNA degradation, the bone mineral of interest would have been turned into water-soluble brushite and thus would no longer have existed.

Further, a more or less intact micromorphology that can be assessed by histological techniques indicates the absence of microorganisms, which is also favorable to DNA preservation.

Finally, empirical findings indicate that preservation of DNA seems to be favored not only by the density of the bony material (compact versus spongeous bone) but also, possibly even more so, by location in a distal anatomical region, i.e., far from the torso with its large amounts of soft tissues. If these findings prove to be reproducible, this would result in enormously helpful guidance in the decision how to sample a skeleton. It would also indicate that the very early autolytic processes of body decay are possibly greatly underestimated as a factor in DNA degradation and long-term DNA preservation.

Information from the Genome

All genetic information in a cell is part of the so-called genome, regardless of its informational value, what type of cell organelle it originates from, and its mode of inheritance. In animal cells, the genome regularly consists of two types of DNA which differ from each other in many respects: chromosomal DNA, also known as nuclear DNA (nDNA), and mitochondrial DNA (mtDNA). While nDNA is organized in the form of densely packed chromosomes that are located within the nucleus of a cell, mtDNA is organized in up to ten identical plasmid-like rings within each mitochondrion of the cell. There is only a single nucleus in each cell, but there are many mitochondria per cell; depending on the intensity of the metabolic turnover of the specific tissue, there may be up to thousands.

Both types of DNA, mitochondrial and nuclear, consist of coding and noncoding regions. The coding regions, also called genes, determine protein synthesis, i.e., they are expressed through the phenotype of an individual, which includes visible features as well as invisible ones (with the latter including, e.g., immunological characteristics). However, until now, it has been the noncoding regions of mtDNA and nDNA that have been the focus of ancient DNA research. This is due to the fact that noncoding regions allow a high degree of sequence and length polymorphism, which are the basis for identifying and reconstructing kinship from the phylogenetic to the genealogical level (Budowle et al. 2003; Pakendorf and Stoneking 2005; Rowold and Herrera 2005).

What Does Mitochondrial DNA Tell Us?

Mitochondrial DNA is most suitable for estimating the time of divergence of two or more populations and, for example, for reconstructing migration patterns. This is due to its nonrecombinant mode of inheritance, which implies that all differences found in the mitochondrial sequence are the result of mutation events thought to occur at a constant rate, set by a "molecular clock." Since the sequence divergence of mtDNA represents a measure of time in this sense, it can also be easily understood why it is in principle possible to investigate present-day populations in order to reconstruct events far back in time. Depending on the choice of sequence that is analyzed, it may be feasible to discriminate individuals on the species or subspecies level, or to assign the maternal lineage to a certain population.

Factors that are thought to perhaps affect the precision of the molecular clock are changes in the amount of natural irradiation, e.g., due to volcanic eruptions, and the number and likelihood of back mutations, particularly at so-called mutational hot spots of the mitochondrial sequence. Other caveats that must be considered in the analysis of ancient mtDNA are the possibility of sequence-specific pseudo-mutations due to DNA degradation, nuclear insertions, and the particular high background of contamination through mtDNA – all of which may threaten the authenticity of the results.

Inheritance of the Mitochondrial Genome

The mitochondrial genome is inherited maternally, lacking recombination and therefore representing a so-called haplotype. This is due to the fact that each female oocyte possesses a full set of mitochondria, whereas a sperm needs just a few to generate energy for movement. For quite some time it was thought that the mitochondria of the sperm did not enter the oocyte at all, but there now is evidence that male mitochondria do enter but are identified as foreign and destroyed by the oocyte. If this latter process is not effective, the result is a so-called heteroplasmy; that is, two different sequences with their particular sequence deviations are represented in an individual's mtDNA. Heteroplasmy may also derive from replication errors during cell duplication, a phenomenon particularly often observed and well known from certain C-stretches of the hypervariable regions (Malik et al. 2002). In ancient DNA analysis, it may be challenging to distinguish between true heteroplasmy and an artifactual signal that may occur due to various reasons.

Sequence Polymorphisms

Mitochondrial DNA reveals a comparatively high density of genes. In humans, as many as 37 genes are represented within the total length of 16,569 bp of a single mtDNA genome. Most of these genes are involved in the metabolic turnover of the cell. Due to the nature of a gene, which codes for the synthesis of proteins, only very limited sequence deviations are possible without disrupting function. However, there are two regions within the human and animal mitochondrial genome, so-called D-loops, which are noncoding, i.e., not involved in protein synthesis. One of the D-loops, spanning almost 1,000 bp at the nomenclatoric origin of the mtDNA, is also known as the *hypervariable region* (HVR), because it reveals comparatively extensive sequence polymorphism. Besides base exchanges, there may also be base deletions and base insertions. The sequences of two randomly chosen individuals from a population differ on average at eight nucleotide positions within the HVR. The experimental design in ancient DNA analysis from prehistoric specimens must consider possible further deviations that may lead to mismatches in the primer binding sites, thereby causing amplification failure.

Cambridge Reference Sequence

In order to describe deviations unambiguously, the international scientific community has agreed to refer to a certain reference sequence. This sequence is either known as the Cambridge reference sequence (CRS) or the Anderson reference sequence. It represents the entire sequence of a human mitochondrial genome – the first that was ever analyzed entirely (Anderson et al. 1981). However, the originally published sequence was revealed to contain some rare polymorphism and sequencing errors (Andrews et al. 1999). The sequence belongs to an individual of haplogroup H, which is the major haplogroup in individuals of European descent. Since in phylogenetic terms this means that it is a comparatively young sequence pattern, there are fairly many nucleotide positions in the human mtDNA that are different from the CRS in all other haplogroups found worldwide. Moreover, the CRS mtDNA reveals two comparatively rare deletions in C-stretch regions of the HVR II, which means that the length of the average human mitochondrial genome is 16,570 or 16,571 bp, respectively.

Haplotypes, Maternal Lineages, and Haplogroups

The actual base sequence in the HVR of an individual is named a haplotype and represents the pattern specific to a maternal lineage. All individuals sharing this haplotype are members of the same maternal lineage, i.e., they are directly related in a genealogical sense, which is most likely when the haplotype is rare or even unique. Alternatively, they are at least closely related in a population genetic sense; that is the situation when many people who are not known to belong to the same genealogical family share this haplotype.

The sequence differences found worldwide in the highly polymorphic HVRs of the mitochondrial genome are divided into more than 20 haplogroups consisting of further subgroups. Those groups are clusters of sequences revealing high intragroup similarities. In general, the assignment of a sequence to a certain haplogroup depends on actual bases that are present at certain key nucleotide positions. While more than 95 % of individuals of European descent can be ascribed to one of seven major haplogroups (Richards et al. 1998), a similar percentage of Native Americans are ascribed to four haplogroups (Torroni et al. 1993). Particularly within highly branched ancient haplogroups, a further division into subgroups is common. These subgroups are defined, in turn, through an additional base pattern at further nucleotide positions that is shared by all representatives of the subgroup. Since ancient DNA is suspected to promote the generation of pseudo-polymorphisms due to degradation artifacts, sequence interpretation and any deductions with respect to phylogeny and migration based on the occurrence of rare or novel haplotypes must proceed with care. At least this holds true for PCR-based analyses; results from NGS analyses seem to be less prone to artifacts of this kind.

Phylogeny and Migration

The age and spread of haplogroups enable us to draw conclusions with respect to questions of human phylogeny and worldwide migration pattern (Soares et al. 2010; Oppenheimer 2012). The age of a haplogroup is basically deduced from its heterogeneity, i.e., the degree of sequence variation within the group. Basically, haplogroups that are more widespread and reveal more different branches and subgroups are older than those that are comparatively homogeneous (Fig. 2) (Brotherton et al. 2013).

In this manner, it is also possible to determine the regional origin and migration patterns of a haplogroup that is represented over a geographically widespread area. At the place or region where representatives of the haplogroup originated, the sequence diversity is expected to be higher than in any other region where the haplogroup is found (Watson et al. 1997).

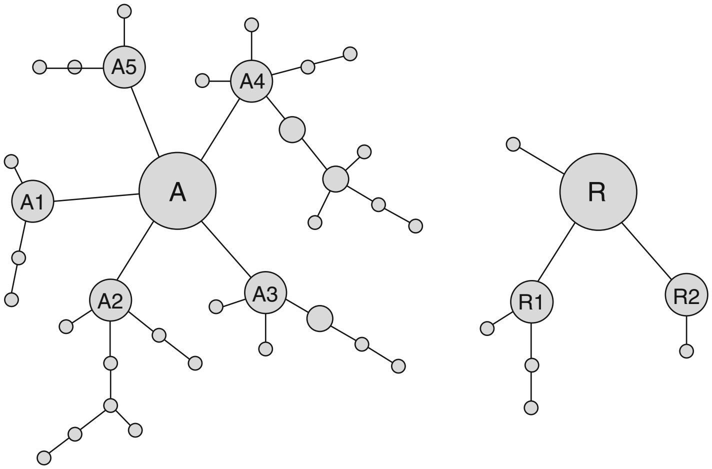


Fig. 2 The degree of heterogeneity of a haplogroup enables us to deduce the age and the geographical origin of the haplogroup. Ancient haplogroups (A) reveal more diversification, including the manifestation of subgroups, while more recent haplogroups (R) are comparatively homogeneous. Each *dot* in this type of depiction represents a single haplotype, each line connecting the *dots* a one-base-pair difference. The sizes of the *dots* correspond to the number of individuals revealing the particular haplotype

What Does Chromosomal DNA Tell Us?

The analysis of chromosomal DNA sequences allows access to the unique genetic pattern of an individual. This pattern is represented by the specific combination of single polymorphic genetic traits, which characterize the individual on a level that enables identification. The number of genetic traits that must be observed to enable identification depends on the degree of polymorphism that is recorded for the observed traits. Most common for identification purposes in the context of, e.g., the reconstruction of genealogical kinship are so-called short tandem repeats (STRs). These markers reveal a comparatively high degree of polymorphism: on average 5–15 alleles of varying lengths are present in a population for each STR. These markers are also suitable for population genetic purposes, although data from many individuals are necessary in order to enable conclusions with respect to phylogeny and migration.

Another target are single nucleotide polymorphisms (SNPs), which are usually biallelic markers revealing a sequence polymorphism at a certain nucleotide position. Unlike STRs, they are not investigated to reconstruct kinship, although this would be possible in principle, but in order to determine, e.g., the immunological properties of an individual. Since the immunological properties of a population are subject to strong selective forces, due to the presence of pathogens influencing morbidity and mortality rates, regional and/or diachronic changes in the allelic frequencies of SNPs allow us to draw conclusions on subjects such as the spread of epidemics or pandemics and everyday living conditions.

In ancient DNA analysis, the accessibility of chromosomal markers is restricted, because of the comparatively low numbers of genomes originally present in a given sample volume. However, optimizations of DNA extraction protocols may compensate for this disadvantage. Once nDNA has been successfully extracted, the analysis of nuclear markers is much less prone to erroneous results due to contamination, given a careful experimental design.

Inheritance of the Chromosomal Genome

The chromosomal genome of an individual represents a novel and unique recombination of its parental organisms. Both parents contribute a so-called haploid set of chromosomes, which are randomly selected from their own diploid chromosomal sets. Therefore, each locus under investigation reveals a maternal and a paternal allele. In the analysis of coding regions, the genotypic level may often be determined without difficulties, but this does not necessarily hold true for the phenotypic level. Gene expression and suppression must be known in order to allow conclusions to be drawn from the genotype of an individual to its phenotype. In ancient DNA analysis, a particular situation that is suspected to be involved in many diseases remains a challenge: the phenomenon of compound heterozygosity. Compound heterozygosity describes a situation where two (or more) mutations, distant from each other on the same chromosome and responsible for a certain morbidity risk, have to be present in a heterozygous state, but one mutation must be located on the maternal, the other on the paternal allele. In ancient DNA with its highly fragmented target sequences, compound heterozygosity cannot be discriminated from a heterozygous state where both markers are mutated either on the maternal or the paternal allele.

Length Polymorphisms and Sequence Polymorphisms

Chromosomal DNA consists of coding and noncoding sequences. From the Human Genome Project it is known that the bulk of DNA is noncoding DNA, sometimes called junk DNA. About 20–30 % of this noncoding DNA consists of tandem repeated sequences. Some of them, the STRs (cf. above), are particularly interesting, since a set of them enables the genetic identification of an individual. Their alleles reveal a length polymorphism which is a function of the number of repetitions of the core unit. In fact, STRs are often identical (e.g., CA_n or $AGAT_n$), but the unique nature of the neighboring sequences enables us to specifically target a certain STR locus. Other than sequence polymorphisms, the variations in fragment length are not suspected to suffer from specific DNA degradation leading to a result that, although reproducible, is still erroneous. However, ancient DNA analysis must be carried out carefully, because STR amplifications also reveal typical so-called stutter artifacts. Since stutter bands occur stochastically, the artifact can be overcome through multiple analyses. Further, the occurrence of this typical artifact can be minimized through optimization of DNA extraction and a sophisticated choice of PCR parameters. Multiple analyses also prevent erroneous homozygous results, which may occur due to so-called allelic dropout when only a small number of intact target sequences are present.

The analysis in ancient DNA of SNPs, which are spread throughout the genome, basically has to deal with the same pitfalls that are suspected to affect the analysis of mitochondrial sequence polymorphisms. Although the risk of non-authentic results due to contamination is much lower than in the analysis of mtDNA and, moreover, can efficiently be monitored through suitable experimental design, the risk of false results due to specific degradation patterns must be considered in the same way as in mtDNA analysis.

Genetic Fingerprints and Identification

The specific allele combinations from analysis sets consisting of 5–15 STRs are also known as genetic fingerprints. As the name implies, the specific allele combinations have an identifying character. Genetic fingerprints are suitable for genealogical kinship reconstruction and for the identification and the assignment of skeletal elements.

In order to be suitable for genetic fingerprinting, the STRs combined in a set have to fulfill two major prerequisites: first, they must be located on different chromosomes in order to avoid haplotypes and to ensure a recombinant mode of inheritance. Second, they must not be linked to genes, in order to avoid the force of possible selective pressure, which would be indicated by strong deviations from a Gaussian allele distribution. If these criteria are fulfilled, the degree to which the value of the so-called matching probability (P_m) can be determined depends on the total number of STRs investigated and on their respective allele frequencies in a given population. The P_m is defined as the likelihood that a second, nonrelated individual reveals the respective allele combination just by chance. Typical P_m values for commercially available and customer-designed sets consisting of 9–15 STRs range from 10^{-10} to 10^{-24}. Of course, these impressive values apply to ideal populations only (panmictic, no selective pressure, etc.). However, the situation in real, possibly even inbred, populations can be simulated approximately when calculating the likelihood that a given set of parents will give birth to two children revealing the same genetic fingerprint. If 10 STRs are observed, the likelihood of this event ranges from 10^{-5} to 10^{-7}. These values indicate that individuals from an inbred population with a limited gene pool are still sufficiently discriminated.

The identifying properties of genetic fingerprints also indicate that STR typing is more suitable than any other strategy to the identification of possible contaminations from a wide spectrum of sources.

Reconstructing Kinship and Paternity Testing

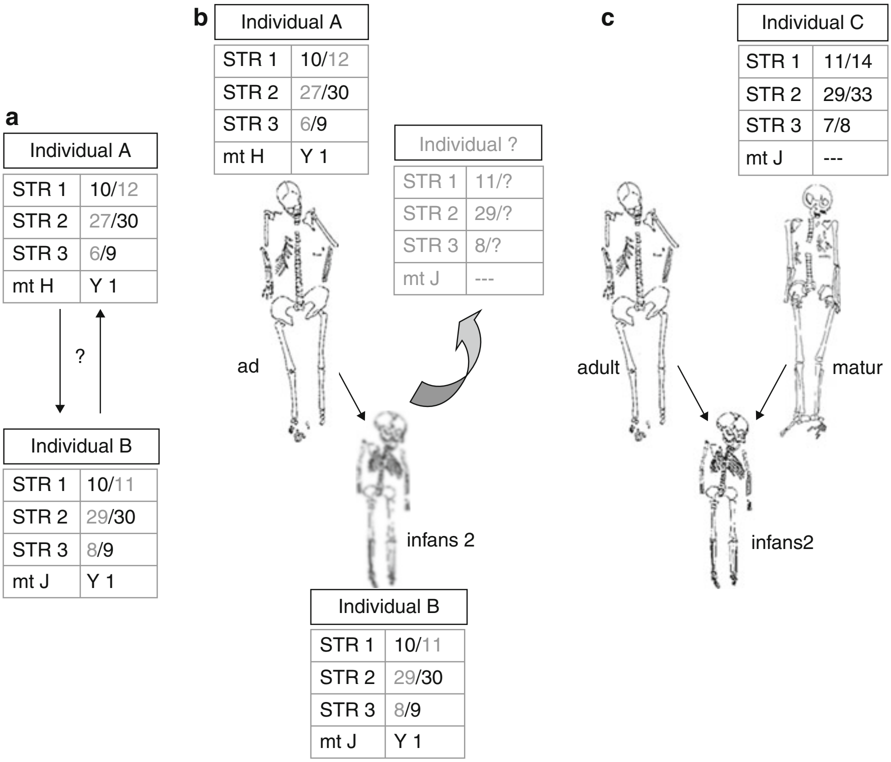
The reconstruction of kinship in a (pre-)historic skeletal series requires a different strategy than if it were a living population. Whereas in a living population, the ages of the individuals help to discriminate a priori the parental generation from the potential descendants, this information is not available in a skeletal series. It is theoretically possible to find the skeletal remains of an individual who died in early adulthood but who fathered an individual who reached the senile age class. Although individuals who are related vertically at first degree share an allele for each observed genetic marker, it is not feasible to deduce from genetic markers who is the parent and who is the offspring. Therefore, infant individuals who have not reached reproductive age play a key role in the reconstruction of kinship (Fig. 3).

If two individuals – infant and adult – are found to share exactly one allele at each observed locus, a paternity (or maternity) test can be constructed as a deficiency case (i.e., one parent missing). If the allelic genotype of a second adult individual of the opposite sex suggests that this may be the missing parent, the likelihood of parentage for both assumed parents is calculated in the manner of two independent trio cases (Brenner and Morris 1990; Chakraborty and Jin 1993). This means that, e.g., in a first step the child-mother dyad is taken as fixed, enabling us to calculate the paternity index for the male individual, and then, in an analogous way, the maternity index is calculated.

In particular, if individuals from a larger burial site are investigated with respect to their genealogical relatedness, the initial search for possible child-parent dyads is facilitated by mitochondrial and Y-chromosomal haplotyping. This strategy permits the assignment of individuals to family lineages. Analogous to autosomal genetic fingerprinting, Y-haplotyping is carried out through STR allele amplifications at the Y-chromosome.

Immunogenetics and Epidemiology: Towards Phenotype

The analysis of nuclear genetic markers that are known to be linked to the immunological properties of an individual is comparatively new. Usually these properties are represented through SNPs, which cause changes in the amino acid



a

Individual A	
STR 1	10/12
STR 2	27/30
STR 3	6/9
mt H	Y 1

Individual B	
STR 1	10/11
STR 2	29/30
STR 3	8/9
mt J	Y 1

b

Individual A	
STR 1	10/12
STR 2	27/30
STR 3	6/9
mt H	Y 1

Individual ?	
STR 1	11/?
STR 2	29/?
STR 3	8/?
mt J	---

Individual B	
STR 1	10/11
STR 2	29/30
STR 3	8/9
mt J	Y 1

c

Individual C	
STR 1	11/14
STR 2	29/33
STR 3	7/8
mt J	---

Fig. 3 If two individuals are found to share an allele for each STR system (=STR 1, STR 2, and STR 3), they may be parent and child. (**a**) From the STR typing and the Y-Haplotype (=Y1), it cannot yet be deduced who is the father and who is the son. (**b**) A morphological or histological age determination not only solves this problem but, moreover, enables us to predict the genotype of the mother, who is still missing. (**c**) If a female individual is found who reveals the respective STR alleles as well as the appropriate mitochondrial haplotype (=mt J), she can be assumed to be the mother. The likelihood of parentage can now be calculated based on the allele frequencies of the investigated STRs

chain, thereby changing protein synthesis. Many of these markers are directly linked to the susceptibility of an individual to bacterial and viral infections and, as a consequence, to his or her susceptibility to certain cancerous growths. These markers are also of interest in the context of heterogeneous reactions of individuals to pharmacological treatments.

The allele frequencies of such markers exhibit considerable deviations worldwide, suggesting that they are subject to selective pressures, as well as genetic drift and bottleneck situations. It is striking that particular European populations or individuals of European descent often reveal allele distributions that deviate strongly from all other human populations worldwide. Not surprisingly, this is interpreted as a result of Europe's unique epidemiological history during the past centuries, and to the selective forces that are linked to epidemic and pandemic infectious disease events (Scott and Duncan 2001).

Many theories and hypotheses that claim to be able to name a particular historic epidemic event bearing responsibility for a certain uncommon allelic distribution are based on more or less thorough linkage studies carried out on modern populations (Stephens et al. 1998; Rannala and Bertorelle 2001). However, some must be classified as mere speculations (Altschuler 2000). In any case, all such studies lack direct proof. Therefore, direct access to historic and prehistoric genotypes will be invaluable. In particular, skeletal series that are known to be linked to epidemics or pandemics can play an important role as genetic archives. However, since the burial sites of skeletal series are often mass graves (e.g., of plague victims), the significant possibility of ancient cross-contaminations due to the special conditions of burials must be borne in mind when setting up the experimental design.

Authenticity

The authenticity of a PCR-based ancient DNA analysis result must be tested in two ways: first, one must exclude the possibility that contamination is responsible for the outcome of the analysis; and second, it must be proved that the result indeed represents the authentic genotype of the (pre-)historic individual sampled, and is not biased due to DNA degradation or analytic artifacts. Depending on the scientific question, the actual sequence that is under investigation, the number of individuals investigated, and, finally, the origin of the samples, proving the authenticity of ancient DNA analysis results may require unique experimental design strategies.

A comparison of PCR with NGS technology suggests that proofs of authenticity may be much more easily brought about for the latter, since NGS technology is not based on exponential amplification. However, if contaminating sequences are of the same species and outnumber the endogenous sequences of the investigated sample, the common strategy to identify contaminating sequences by their minor number is prone to fail with NGS as well.

Contaminations

Since ancient samples usually consist of very few DNA targets, even minor contaminations may cause false results, at least in PCR-based analyses. Contaminations may originate from various sources and may reveal various degrees of degradation. Therefore, there is no simple strategy for how to avoid and detect them.

Basically, we can distinguish four ways in which contaminations may enter the analysis:

- Cross-contamination between the ancient sample materials
- Contaminations of the sample material by former or current investigators

- Contaminations in laboratory reagents and disposable material
- Contaminations of either sample materials or reagents by amplification product carryover from earlier PCR analyses

Cross-Contamination

Cross-contamination of the sample material may in principle happen at any time. However, two situations in particular are suspected to increase the risk of sample cross-contamination: burials at a non-individual site (e.g., mass graves) and the laboratory processing of the samples (e.g., transfer of sample material through unclean laboratory devices or handling mistakes). Cross-contaminations are particularly hard to detect, since all sequences involved would reveal a degradation pattern as expected for ancient DNA. Further, their occurrence cannot be detected through use of the classical set of negative control samples, which includes no-template controls and extraction blanks. A possible cross-contamination event must therefore be detectable in the analysis result itself, as would be the case, for example, if amplification of DNA fragments showed up three or four alleles instead of one or two, clearly indicate the presence of material from a second individual.

Contamination by Investigators

This type of contamination may in principle happen anytime a sample is handled. What the contamination pattern looks like depends on the amount of contaminating cells and on whether the contamination happened recently or decades ago. It may vary from comparatively easily identified, fully intact DNA profiles to a hard-to-recognize type which resembles the typical cross-contamination. As in the case of cross-contaminations, negative control sample sets are not suitable for monitoring this type of contamination. Again, the analysis result itself must reveal indications of the problem. Unlike the case of a classical cross-contamination, contamination by an investigator is most likely (but not necessarily) a superficial one. Therefore, thorough removal of the sample surfaces minimizes the risk of this contamination type. This applies to both PCR-based analyses and NGS-based analyses.

Contaminations in Laboratory Reagents and Disposables

Laboratory reagents may already be contaminated when purchased (e.g., primers, reaction mixes), or they may become contaminated through handling by the investigators. In both cases, the degradation patterns of the contaminating DNA and the amount of contamination may vary strongly. If premixed PCR reaction components are used, particularly bovine serum albumine (BSA), which is a component enhancing the *Taq* DNA polymerase, may cause severe problems, due to residues of bovine DNA. This can be shown through cytochrome *b* sequence amplifications that indicate the species. However, this type of contamination can be monitored through suitable sets of negative controls. Ideally, the analysis result from the sample material itself will also provide information indicating possible contaminations.

The situation is completely different where disposable laboratory materials are concerned. PCR reaction tubes turn out to be regularly contaminated right from the production process, with human DNA prevailing (Hauswirth 1994; Schmidt et al. 1995, Gill et al. 2010), although DNA of bovine origin has also been found (Hummel 2003a). The percentage of reaction tubes that suffer from contamination varies depending on the supplier, the brand, and the actual lot. The vast majority of these contaminations are of mitochondrial origin. The reason for this lies in the nature of the production process, which very often includes autoclaving steps. If there are just a few reaction tubes containing cellular contaminations at this stage of the manufacturing process, these cells will become lysated by the autoclaving temperature and, as a result, hundreds of thousands of mitochondrial genomes are distributed more or less uniformly. Typically, the number of tubes that show specific signals of mtDNA after 40 amplification cycles varies between 20 % and 80 % if fragments of less than about 150 bp are amplified. The reason why autoclaving is still part of the manufacturing process, even in so-called high-performance (e.g., "PCR clean," "DNA free") and high-price brands, is that this allows producers to guarantee that they are staying below a certificated level of DNA for each tube in the lot, without having to invest in the cost of a truly DNA-free manufacturing process.

All kinds of treatments applied to amplification reaction tubes (e.g., UV treatment, bleaching, rinsing with and without ultrasonic treatment) are inefficient in the sense that they cannot overcome the problem. At best, a more or less sizable reduction in the number of tubes revealing contaminations can be achieved. Since the contaminating mtDNA in reaction tubes consists of just a few targets per tube, and because it is typically just as degraded as ancient DNA, it is usually not even noticed in modern DNA applications. For ancient mtDNA applications, however, which may also start from just a few intact targets, it is the most severe contamination problem of all, since it is unavoidable and may be hard to detect. Typical sets of two or three negative controls in a PCR set-up are uninformative, simply due to their small number. If they stay blank, this is not necessarily representative of the tubes in which the samples were processed. Then again, if the negative controls do reveal signals, these cannot either be assumed to apply to the tubes in which the samples were analyzed.

A way to improve the situation in mtDNA analysis is through numerous reproductions of the analysis, ideally amplifying only fragment lengths considerably greater than 200 bp. In order not to have to discard too many analysis results which reveal ambiguous signal patterns and are suspected of deriving from a mixture of precontaminating tube DNA and ancient sample DNA, researchers are advised to carry out checks with at least 30 negative controls each time a new lot of reaction tubes is in use.

Further, depending on the target sequence and the number of samples intended to be analyzed, it may be preferable to choose a NGS-based approach for the analysis of mitochondrial genomes.

Another option, although extremely laborious and inconvenient, is the use of glass tubes for PCR amplifications, manufactured from high-temperature-resistant glass. These can be reused after being tempered for a couple of hours at 600 °C at least. It may be necessary to elongate the steps of the amplification cycle for efficient reactions carried out in glass tubes; however, if tempering has been done these reactions will be positively free of contamination.

Contamination Through Product Carryover from Earlier PCR

Product carryover, although a disaster if it occurs, is not a particular threat to ancient DNA analysis. This is because it is comparatively easy to detect and easy to prevent if some basic rules are strictly followed. Product carryover would block the easy and low-cycle amplificability of a certain marker, while other markers of similar fragment length would not yet be amplifiable. Also, as long as more than a single sample is contaminated (which is extremely likely in the case of product carryover), a series of samples would reveal identical analysis results if, e.g., an extraction buffer was contaminated. If product carryover found its way into a PCR reagent, the entire set of negative controls would all show signals, thus reacting in exactly the same way the samples do.

A method to efficiently prevent product carryover contaminations, which is practiced in almost every ancient DNA laboratory, is the strict separation of pre- and post-PCR areas, including strict dedication of all equipment, such as pipettes, centrifuges, deep freezers, and so on.

Degradation and Analysis Artifacts

Ancient DNA results may also be non-authentic due to degradation and analysis artifacts. That is to say, even though it was the authentic ancient DNA that was analyzed, the original sequential order of bases or the original fragment lengths may have been biased. If one counted up the number of publications that report degradation phenomena, one might believe that non-authenticity due to degradation artifacts is a critical point almost exclusively with respect to the base sequence, rather than fragment length (Gilbert et al. 2003; Binladen et al. 2006). This reporting pattern, however, most likely reflects a bias as well, since only very few ancient DNA working groups have long-standing experience with fragment length analysis, which is mainly linked to autosomal and Y-chromosomal STR typing (Keyser-Tracqui et al. 2003; Hummel et al. 2000; Hummel 2003a). The bulk of the discussion of typical fragment length artifacts is taking place in the forensic sciences context, where STR typing of degraded DNA samples has been routine for many years (Butler 2005).

Non-authenticity of the Base Sequence

Base degradation is one of the major reasons why the analysis even of authentic ancient DNA may nevertheless reveal erroneous results. The most numerously occurring artifacts are reported to be the transition C > T/G > A and A > G/T > C; others have been observed much more rarely or not at all (C > G/G > C), at least not in nDNA (Binladen et al. 2006). Another important aspect is the question of whether mtDNA and nDNA are affected to the same extent in this. Although nDNA is thought less likely to suffer from degradation artifacts, owing to the protection the nucleic acid sequence receives from histones, an investigation by Binladen et al. (2006) could not detect major differences. Due to its obvious relevance, the C > T transition is most often discussed with respect to the cause of the artifact (cytosine may degrade to an apparent uracil, of which the complementary base is an adenine, which in turn would lead to the introduction of a thymine during the next elongation phase), its likelihood of occurrence, and available methods to overcome the artifact. One common strategy to prevent the amplification of DNA fragments containing apparent uracils is an enzymatic treatment of the DNA extract prior to amplification (Haak et al. 2005). This strategy claims to destroy all DNA fragments that contain uracil-like degraded cytosines – but it may result in total destruction of all potential target DNA sequences for the intended amplification. Further, transitions others than the C > T transition are not affected by this approach.

Therefore, other strategies to overcome generation of non-authentic PCR-based results due to DNA degradation would be preferable, if available. These could be valid strategies for DNA repair or unbalanced initial PCR employing a single primer that results in a linear amplification of one strand only. Furthermore, in cases where the sample itself does not represent a mixture of DNA from different individuals, a combination of cloning strategies – which often suffer from too few clones being analyzed (Bower et al. 2005) – and direct sequencing could be informative.

Another way to monitor and evaluate analysis results that are suspected to be biased by degradation artifacts could be the implementation of cross-checks through amplification of further loci which basically provide the same information, or at least parts of this information. In the case of mtDNA haplotyping, a suitable option might be the analysis of SNP markers on the mtDNA genome, which are known to be linked to haplogroups (Torroni et al. 1992). In the case of nuclear SNPs, the targeted loci for cross-checks might be additional polymorphic sites which are also known to be linked to certain genes, although possibly with a lower linkage rate.

Non-authenticity of Fragment Lengths

Typical fragment length artifacts are so-called stutter bands and allelic dropout. Both of these kinds of artifacts, which occur in the course of STR amplifications, are well known and extensively discussed in the ancient DNA and forensic literature (Butler 2005; Hummel 2003a). Unlike sequence degradation, allelic dropout and stutter artifacts are not a direct degradation phenomenon but rather an indirect one, since the likelihood that they prevail in the data, leading to an inaccurate analysis, depends on the number of intact targets that are submitted to amplification. Although a reduced number of intact targets is characteristic for ancient DNA extracts, these artifacts can occur during amplification of modern intact DNA as well, if there are few targets throughout the first amplification cycles. But even when very few targets are submitted to the reaction, the generation of fragment length artifacts constitutes a stochastic event that is – except in the case of base degradation – not due to alterations of the target but an amplification artifact. Consequently, mere multiple repetition of the analysis will allow the experimenter to evaluate the authenticity of a result, on the basis of reproducibility. Moreover, strategies are available to lower the tendency of the amplification reaction to create these types of artifacts. The most obvious one is to optimize the DNA extraction, in order to increase the number of targets. This helps in particular to avoid allelic dropout. In order to minimize the generation of stutter bands, relaxation of the elongation temperature has proved to be successful. However, since *Taq* DNA polymerase activity is damped down by a lowering of the temperature, the time allowed for elongation should be correspondingly prolonged.

In any case, the fact that STR amplifications are regularly carried out in multiplex approaches means that cross-checks are already built into the analysis, since the evaluation of authenticity is clearly simplified when based on the patterns of the entire set of amplified loci (Fig. 4).

Basic Strategies in Experimental Design

There is no general strategy for how to carry out an ancient DNA analysis; the most decisive factors for the experimental set-up are the sample material itself, the underlying scientific question, and the properties of the DNA sequence in focus. These factors should be considered in making decisions on the need for pre-experiments (e.g., checks for contamination rates in amplification tubes), the choice of appropriate sets of negative and positive controls, and the design of the amplification and analysis strategy. The final experimental strategy ideally combines two aims: maximizing the likelihood of a result, and maximizing the likelihood that this result can positively be proved to be authentic (Fig. 4).

Authentic results are achieved through entirely different strategies depending on, for example, whether human or animal DNA is under investigation, whether a single sample or series of samples are analyzed, whether mitochondrial or nDNA is the target, and whether base sequences or fragment lengths carry the desired information. It is unhelpful, therefore, to focus overly on abstract criteria for ancient DNA analysis per se, such as have been proposed in the past (Cooper and Poinar 2000). These broad criteria do not refer to any specifics of the research context; an experimental design following these published regulations would only directly meet the demands of the analysis of human mitochondrial HVR DNA from a single sample. But even for that particular scenario, observance of these standard criteria and regulations would not, in itself, result in full proof of authenticity, since cross-contaminations and contaminations by earlier investigators could never be ruled out.

Sample Preparation

The preparation of ancient DNA samples has to be devoted to two main objectives:

- Removal of possible contaminations
- Optimal preparation of the sample for DNA extraction and further amplification reactions in subsequent analytic procedures

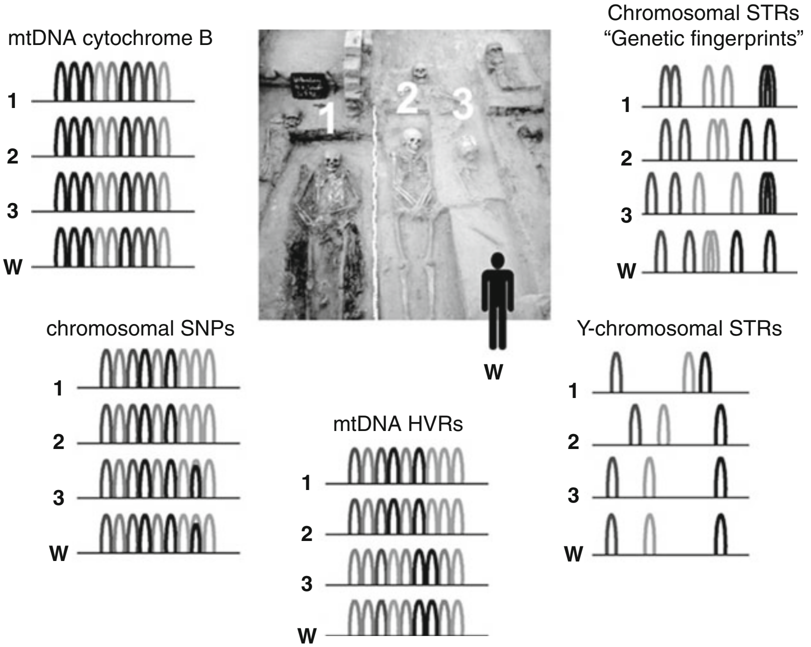


Fig. 4 Authentification power of genetic fingerprinting. The analysis strategy should consider the number of individuals that are being investigated, the number of people who worked on the sample material, and the underlying scientific question, including the sequence of interest, as shown in this example. Given that three skeletons (1–3) are being investigated and one person (W) is working on the samples, the analysis of different genetic markers may potentially have different results, therefore requiring different sets of control samples and cross-experiments. If, for example, a cytochrome *b* fragment is amplified, all samples, including ones from W, would reveal the same base sequence, and there would be no proof that W did not contaminate the samples. If a nuclear SNP is investigated, e.g., samples 1 and 2 may be homozygous, but sample 3 and W heterozygous. Again, the results do not exclude the possibility that samples 1 and 2 are cross-contaminated, or that W may have contaminated sample 3. The same may hold true for the investigation of mitochondrial HVRs. In the given example, analysis of the Y-chromosomal haplotypes can exclude cross-contamination between samples 1 and 2. However, only the investigation of autosomal STRs that represent individual genetic fingerprints enables us to prove that no contamination events are responsible for the ancient DNA results. While in all analyses except genetic fingerprinting, even extended sets of negative controls are not able to rule out direct contamination of sample 3 by W, autosomal STR typing would not even need a negative control to exclude contamination events such as carryover, contamination through laboratory personnel, and cross-contamination

Where superficial contaminations are concerned – i.e., most commonly, contaminations by present or former investigators – the first objective is achieved by thoroughly removing the surface of the sample. Further possible contaminations may also be removed by rinsing the sample surface with a strong oxidative reagent such as, e.g., household bleach. How the second objective is achieved depends on the sample material. However, in general, any increase in surface area through, e.g., crushing of the sample prior to chemical treatment has proven to improve later analysis results. Further, depending on the actually chosen extraction technique, factors such as centrifugation forces and the relation of the sample material to incubation buffers and reagents are also crucial. We recommend the development of a standard protocol with respect to given sample properties before valuable sample material is processed.

Optimizing DNA Extraction

Optimal DNA extraction protocols are obviously a highly individual matter, dependent as they are on the exact biochemical state and composition of the sample material. However, standard protocols offer a valuable starting point. The basic aims of standard protocols are:

- Maximization of the amount of DNA
- Minimization of DNA degradation in the course of the extraction procedure
- Minimization of the presence of inhibiting substance residues in the DNA extract

At present, these goals seem best achieved through automated DNA extraction using magnetic beads, although the amount of DNA in the extracts lags somewhat behind what, e.g., phenol-chloroform procedures will accomplish. However, the advantage of the DNA extracts being practically free of inhibitors, as can be demonstrated through real-time PCR, may outbalance the possible loss of DNA. In case the sample material consists of very little intact target DNA and only minor amounts of inhibiting components, other strategies – such as retention of the DNA on silica-coated membranes – may be superior with respect to optimum DNA yield. In general, the use of any type of automation at this stage of sample processing is advantageous, since it minimizes the handling of the samples and thus the risk of contamination.

Amplification Strategies

In general, there is no optimal amplification strategy; instead, the basic experimental design must be deduced from the scientific question and the sequence of interest (Fig. 4). However, there are some key aspects which should be considered.

First, the more the investigated sequence is characterized by polymorphisms, the fewer cross-checking experiments are necessary. Ideally, the amplification result will be “individual,” in the sense of identifying a unique individual, since this enables an efficient check for any type of possible contamination. If, for example, nuclear STR typing is carried out, only a minimum of negative controls are necessary. It may be advisable to deviate from classical amplification parameters, in particular concerning the elongation temperature. A decrease in the elongation temperature, or a shift to a two-step PCR consisting of a denaturing phase and a prolonged annealing phase only, may result in a remarkable decrease in stutter bands, which are an STR-specific amplification artifact encountered even in modern DNA amplifications (cf. above).

Second, in case the markers of interest are polymorphic but far from revealing results specific to an individual – as would hold for any type of biallelic SNPs or short deletions – the aim should be to link the analytic result to another, identifying one. This is realized through integration of the primers for, e.g., the SNP amplification to a multiplex assay designed for STR-based genetic fingerprinting. This approach has proved successful for nuclear markers (Bramanti et al. 2000; Fulge 2005; Hummel et al. 2005; Puder 2005), although it may require multistage fragment-length determinations, including a restriction fragment length polymorphism (RFLP) analysis. If the biallelic markers are multiplexed with nuclear STRs, only a minimum set of negative controls is necessary.

Third, the amplification of mtDNA, which is regularly represented in ancient DNA extracts by a greater number of intact targets, is hard to carry out using the same technique as for the amplification of nDNA. One reason lies in the different demands for optimal amplification cycles. Moreover, the aim of mtDNA investigations is usually a sequence analysis, which, for technical reasons, cannot be combined with STR typing. We highly recommend re-checks of contamination rates for different brands of amplification tubes. These should be carried out with the primers that are intended for the actual investigation, using high cycle numbers (>45). If possible, the primers should reveal sensible mismatches against species that are not intended to be amplified but are suspected to be present as contaminating targets (humans, working animals). It may be necessary to launch experiments that check sequence-specific degradation patterns. Although mtDNA is regularly represented by more targets than chromosomal DNA in an ancient DNA extract, the particulars of the situation with respect to degradation pattern and contaminations in amplification tubes will significantly complicate the proof of authenticity. Due to these facts and the non-individual character of the polymorphisms, even in the HVRs of mtDNA well-adapted sets of control samples are necessary, since typical sets of negative controls do not apply.

Enhancing Specificity and Sensitivity of a PCR

The specificity of a PCR, i.e., the exclusive amplification of the targeted sequence, is a basic prerequisite for success, in particular if the subsequent analysis includes a so-called Taq cycle sequencing reaction. PCR specificity can be challenging to achieve. However, any other type of ancient DNA analysis also suffers from the generation of unspecific by-products. This holds true even if no confusion with the target sequences is possible, due to, e.g., entirely different fragment lengths. The reason is that sensitivity decreases as soon as by-products, including primer dimers, are generated in the amplification reaction, since the resources for the reaction (Taq polymerase activity, primers, dNTPs, and buffer) may be exhausted sooner in this competitive situation. The consequence is that the target product, though present, may not reach the detection limit, because the by-reaction has already led to attainment of the amplification plateau.

Although optimization of the annealing temperature positively influences the specificity of the amplification reaction, even this step may not result in a highly specific reaction, or may compromise the reaction efficiency, if the annealing temperature approaches the melting temperature of the primers.

A particularly effective means to increase the specificity and therefore the sensitivity of the reaction is given through primer design. The criteria for a good primer design can be summarized as follows.

- Primers should reveal a minimum length of 20 bp if possible, preferably 23–30 bp.
- The binding energy of the 5′-end must increase that of the 3′-end in order to enable elongation only if the entire primer matches.
- 3′-end primer dimers and hairpin formation must be strictly avoided, since these formations will be elongated and cause generation of by-products.
- Primers should not reveal possible mismatches to the intended target caused by sequence polymorphism within at least 3 bp from the 3′-end.

If a primer pair meets these criteria, the amplification product increases considerably in quality and quantity. Further improvement in reaction efficiency can then be achieved through a step-wise decrease of the annealing temperature. Especially if only a very few intact DNA targets have been extracted from the sample material, this measure is likely to constitute the difference between an amplification failure, on the one hand, and a weak amplification product ready for further analysis, on the other.

Conclusion

Over the last two decades ancient DNA analysis has evolved from an enthusiastically publicized yet controversial technique revealing some spectacular results to a sound practice generating biological data that help explain the past. For quite some time this positive development was not foreseeable, because the high sensitivity of the PCR technique is both its greatest advantage and its most significant drawback. The discussion was dominated by the question how to fully authenticate PCR results and how to optimize experimental strategies.

We are now witnessing the early stages of the development of Next Generation Sequencing (NGS) approaches, which give access to entire genome information. The coming years will prove how well these very promising alternatives to PCR will come through their own teething troubles.

Cross-References

- ▶ Genetics and Paleoanthropology
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Investigation on Extracellular Matrix Proteins in Fossil Bone: Facts and Perspectives
- ▶ Molecular Evidence on Primate Origins and Evolution
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Modern Humans
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Population Biology and Population Genetics of Pleistocene Hominins
- ▶ Prospects and Pitfalls
- ▶ The Evolution of Speech and Language

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Modeling the Past: The Primatological Approach

Robert W. Sussman and Donna Hart

Contents

Abstract

Many models have been developed to depict the behavior and ecology of our earliest relatives. However, the Man the Hunter model has been the most widely accepted way of viewing human evolution. This theory gained ground in the mid-twentieth century and has been recycled ever since under various guises in the scientific and popular literature. Many human traits, such as bipedalism, monogamy, territoriality, tool use, technological invention, male aggression, group living, and sociality, are often linked to this perspective. Although theories and associations of human aggressive hunters abound, they are rarely based

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R.W. Sussman (✉)
Department of Anthropology, Washington University at St. Louis, St. Louis, MO, USA
e-mail: rwsussma@artsci.wustl.edu

D. Hart
Department of Anthropology, University of Missouri, St. Louis, MO, USA
e-mail: hartd@umsl.edu; hartd@msx.umsl.edu

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on the two evidentiary approaches that shed light on early hominin ecology and behavior – living primate models and the fossil record. Here, an outline is given on a methodology of reconstructing early human behavior by using both the fossil record and extant primate ecology and behavior. Data on early human fossils, on modern primates living in similar habitats to our earliest ancestors, and on rates of predation both today and in the distant past indicate that Man the Hunted may be a more accurate descriptor of our earliest relatives. Here evidence for the Man the Hunted theory, some of the behavioral patterns that were needed to protect our earliest ancestors from predation, and how this may lead to a new perspective on certain aspects of human nature are described.

Introduction

In the early 1950s, the once thought missing link to our earliest human ancestor, the Piltdown Man, was confirmed to be fake (Weiner et al. 1953), and most scientists were beginning to believe that australopithecines were indeed hominins. It was becoming obvious that our earliest ancestors were small brained and probably more like nonhuman primates than modern humans in much of their behavior and ecology. The idea that there was a major "gap" between ancestral humans and nonhuman primates was no longer considered tenable, and the continuity between ourselves and our ancestors was emphasized. This stimulated scientists to begin thinking about using the living primates as potential models for the reconstruction of the behavior and ecology of our earliest ancestors. One of the first attempts at this was by Bartholomew and Birdsell (1953). Since then many models have been proposed.

Reconstructing the Behavior of the Earliest Hominins

There has been much debate about which type of model might best be employed in reconstructing the evolution of early human behavior. Tooby and DeVore (1987) describe three different types of models that have been used. The first is what they designate as referential models. In this case, a living species is used as a literal model for an extinct taxon (the referent species). For example, chimpanzees often are seen as the best referents for early hominins (e.g., Stanford 1999; McGrew 2010). Second is the conceptual model, in which a mosaic of morphological or behavioral traits is seen as a broad analogue to reconstruct early hominin species. As an example, one living primate species might be used to reconstruct the diet and another to reconstruct the social behavior. Tooby and DeVore label the third type as strategic modeling. In this case, it is assumed that species in the past were subject to the same fundamental evolutionary laws and ecological forces as species are today. Although no present species will correspond precisely to any past species, the principles that produced the characteristics of living species will correspond exactly to the principles that produced the characteristics of the species living long ago.

There has been a great deal of disagreement as to which of these three types of models might produce the best results (e.g., Kinzey 1987; Potts 1999; Stanford 1999; Jolly 2001; Elton 2006; Sayers and Lovejoy 2008; McGrew 2010; Van Reybrouck 2012) or even whether labeling these models diminishes their usefulness. In the model presented in this paper, there is an attempt to use all of the above in what is considered a logical and appropriate manner but always taking into account whether any particular aspect of our model is inconsistent with the evidence presented in the fossil record. This brings up the question of what kinds of evidence should be used, and in what manner, in attempts to reconstruct the behavior and ecology of our earliest ancestors.

The most important evidence is the fossils of hominins themselves; careful examination and understanding of the actual skeletal remains of the creatures. However, useful evidence would also include other fossil materials (such as tools or footprints) left by our earliest relatives and clues about the environment in which they lived (such as fauna, flora, or water sources). While fossils provide the most important data for an accurate reconstruction, many current theories of early hominin behavior fall short in their critical examination of the fossil evidence. In fact, they are often virtually fossil-free.

Besides fossils, any other types of secondary evidence used in reconstructions are less reliable but, nonetheless, offer insights. These should be ranked in the following order as far as applicability to reconstructing early hominin lifestyles: (1) The behavior of nonhuman primates living under similar ecological conditions to those of our earliest ancestors (e.g., Elton 2006). It is best to keep timing in mind with this approach. Forests change and so do climates and so do species, as well. Hominins likely began as edge species (living in a mixture of wetlands and grasslands) but moved out onto more open savanna about 2.5 mya (Reed and Eck 1997; Reed 2008). (2) The behavior of our genetically closest primate relatives, such as chimpanzees, bonobos, and gorillas (e.g., McGrew 2010). However, lumping all the great apes together as one analogue when they are so diverse is dangerous, although some characteristics may remain conservative within a taxonomic group. For example, monogamous pair bonds among the lesser apes or gibbons, or upright posture among the apes, might be considered phylogenetically conservative traits shared by all or most species within a taxon. (3) Characteristics shared by certain (or all) modern humans that might also be similar to our earliest ancestors. Modern foragers, however, are just as advanced and evolved within their own culture and environment as any Western urban dwellers. The least confident recommendation is (4) the behavior of other animal species that might be living under similar conditions or that share some aspects of the lifestyle of early humans, such as certain carnivore or prey species. However, a cat is still a carnivore even if it eats some grass; early hominins included a few vertebrates in their diet, but they cannot legitimately be compared to obligate meat eaters.

In using any of these types of secondary evidence, it is necessary to be extremely careful (because in many cases, similar-looking behaviors are not the same); we can end up comparing apples with oranges, lions with hominins, or even strangler figs with purse snatchers! (Yes, the analogy of invasive rainforest fig trees to purse snatching muggers has been made in the sociobiological literature (Ghiglieri 1999).) Obviously, words with loaded meaning for humans – war, rape, murder, infanticide, and genocide to name a few – must be used with extreme caution when referring to the activities of nonhuman species. In this regard Jonathan Marks (2002, p. 104) warns against "... a science of metaphorical, not of biological, connections."

One cannot, therefore, necessarily impute correlation between human ancestors and data based on extant carnivores, modern human foragers, or great apes. For example, even the concept of hunting in chimps and humans is quite different. Present-day human hunters purposely search for animal prey, but chimpanzees do not: "Instead, they forage for plant foods and eat prey animals opportunistically in the course of looking for fruits and leaves" (Stanford 1999, p. 48). Furthermore, reconstructions must always be compatible with the actual fossil data – the fossils are real but the models we construct are hypothetical and must constantly be tested and reconfirmed. Lastly, when attempting to construct models of our early ancestors' behavior, it is necessary to be precise about timing (Tattersall 2010). If one says our earliest human ancestors (those who lived seven million years ago) behaved in a certain way, we cannot use fossil evidence from two million years ago, nor can we confuse those creatures from two million years ago with those who existed 500,000 years ago. As a case in point about timing, one poses the question: Could hunting have occurred without tools? The first evidence of stone tools comes from around 2.6 million years ago (Semaw 2000). The earliest hominin fossils, however, date from almost seven million years ago (Brunet et al. 2002), at least four million years before the first stone tools.

The most popular and currently accepted theory of human evolution is the Man the Hunter model. In seeking to understand why this model is so captivating and easily adopted as the paradigm for human evolution, it is instructive to remember that the first hominin fossils to be found in the nineteenth century were European specimens well under 100,000 years in age, and most of the artifacts found with them were finely crafted spearpoints or tools used for slaughtering animals. The Paleolithic cave paintings in Europe also depicted a metaphysical connection between humans and hunting. Nevertheless, when one looks at the fossil evidence, hunting came quite late to our human family. Interpretations of hominin behavior, therefore, should be conservative and cautious, as stated by Klein (1999, p. 306): "... the mere presence of animal bones at archaeological sites does not prove that hominins were killing animals or even necessarily exploiting meat. Indeed, as was the case in the earlier South African sites, the hominin remains themselves may have been the meal refuse of large carnivores."

The diversity of large carnivores was extensive in the African paleo-past. Many groups of carnivores that are now extinct (such as the huge short-faced bear, *Agriotherium africanum*) may have preyed on hominins between 6 and 3.5 mya. Then at about 3.5 million years, new carnivores evolved to join the previous groups, meaning that as many as eight to ten different species of saber-toothed cats, false saber-toothed cats, conical-toothed cats, giant hyenas, and large wolflike canids were roaming the same African sites where hominin fossils have been found (Treves and Palmqvist 2007) (see Fig. 1).

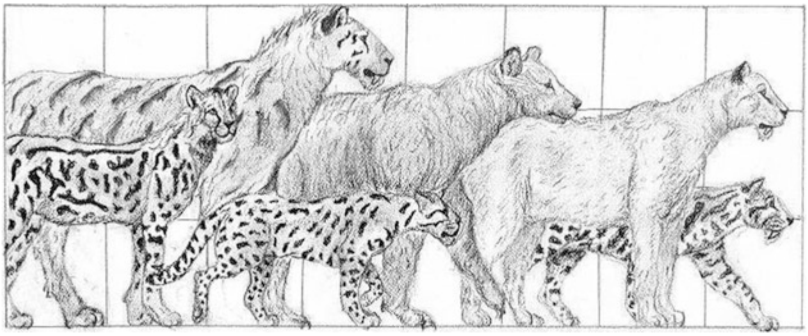

Fig. 1 (*Large Plio-Pleistocene predators*). Relative sizes of fossil cats and bears from the time period 8.5 million to 1 million years ago. Each *square* approximates 20 in. on each side; three *squares* equals 5 ft. From *left* to *right*: giant cheetah (*Acinonyx*); saber-toothed cat (*Machairodus*); ancestral leopard (*Paramachairodus*); bear (*Indarctos*); saber-toothed cat (*Homotherium*); saber-toothed cat (*Megantereon*) (C. Rudloff, redrawn from Turner 1997)

The transition to hunting as a dominant way of life does not appear to have started until after the appearance of our own genus, *Homo*, and may not have even begun with the earliest members of our genus. *Homo erectus* has been given credit in the past for existing as a large animal hunter, and dates as far back as 1.75 mya have been hypothesized for such a lifestyle. But if you take a conservative approach to this subject – looking only at facts and fossils and not imaginative speculations – the first indications of hunting are amazingly recent. In fact, according to some paleontologists, the first unequivocal evidence of large-scale, systematic hunting by humans is available from paleoarchaeological sites possibly only 60,000–80,000 years old (Binford 1992; Klein 1999). The earliest hominin fossils are 6–7 million years before the first factual evidence of systematic human hunting.

No hard archaeological evidence, in other words no fossil evidence of tools designed for hunting, exists earlier in time than a finely shaped wooden spear excavated at Schöningen, Germany, dated at approximately 400,000 years of age (Dennell 1997; Thieme 1997). The famous Torralba and Ambrona sites in Spain, dated at 500,000 years ago, contain huge numbers of large mammal bones. They were thought to represent unquestionable evidence of megafauna killed by Pleistocene hunters. Now these two sites are being reconsidered in light of better archaeological analysis. Elephant bones at these sites could just as likely represent natural deaths or carnivore kills as they do the remains of human hunting (Klein 1999; Klein et al. 2007). Further, no hominins were large-scale hunters before they had the use of fire (because of their dentition and alimentary tract, points we will elucidate below), although insects, small vertebrates, lizards, and birds likely were eaten opportunistically. The best evidence for the controlled use of fire appears approximately 800,000 years ago in Israel (Goren-Inbar et al. 2004). Klein (1999, p. 160) states: “The assumption of consistent hunting has been challenged, especially by archaeologists who argue that the evidence does not prove the hunting hypothesis . . . it is crucial to remember (although not as exciting) that probably the majority of calories [came] from gathering plant foods."

Dentition and Diet

Whether *Homo erectus* or any other hominin before 800,000 years ago regularly hunted or scavenged may be a moot question. Hunting would only be an activity undertaken if early hunters could eat what they killed, and to eat raw meat, it is necessary to have teeth capable of masticating and processing meat.

Obviously, Man the Hunter models of human evolution assume that a significant portion of our earliest ancestors' diets must have come from killing and eating meat from relatively large mammals. By comparing the characteristics of the dental and jaw morphology of various living primates with those of fossils, one can make inferences about the diets of early hominins. Teaford and Ungar (2000, see also, Ungar 2011) carried out just such a comparison in an attempt to reconstruct the early hominin diet. Using such features as tooth size, tooth shape, enamel structure, dental microwear, and jaw biomechanics, they found that the earliest humans had a unique combination of dental characteristics and a diet different from modern apes or modern humans. Ungar (2004) extended this analysis by examining occlusal slope and relief of the lower molars.

Australopithecus afarensis is characterized by jawbones that are thick, with relatively small incisors and canines in relation to molars. The molars, by comparison with other primates, are huge, flat, and blunt, show less slope and relief, and lack the long shearing crests necessary to mince flesh. *A. afarensis* also had larger front molars than back molars. The dental enamel is thick, and microwear on the teeth is a mosaic of gorilla-like fine wear striations (indicating leaf eating) and baboon-like pits and microflakes (indicating fruits, seeds, and tubers in the diet). These definitive pieces of evidence coming from fossil dentition all point away from meat eating.

In studies of mid- to large-sized primates, such as macaques, baboons, chimpanzees, and modern human foragers, in which the amount of time spent obtaining animal protein has been quantified, the total is very low, usually making up less than 5 % of time spent feeding (Garber 1987; Sussman 1999). Given these facts, it is hypothesized that early humans were able to exploit a wide range of dietary resources, including hard, brittle foods (tough fruits, nuts, seeds, and pods) as well as soft, weak foods (ripe fruits, young leaves and herbs, flowers, and buds). They may also have been able to eat abrasive objects, including gritty plant parts, such as grass seeds, roots, rhizomes, and underground tubers. As stated by Teaford and Ungar (2000, p. 13508–13509): "this ability to eat both hard and soft foods, plus abrasive and nonabrasive foods, would have left early hominins particularly well suited for life in a variety of habitats, ranging from gallery forest to open savanna." Dental morphology indicates that the earliest hominins would have had difficulty breaking down tough pliant plant foods, such as soft, fibrous seed coats and the veins and stems of mature leaves, although these foods may have been eaten occasionally (Ungar 2011). Interestingly, Teaford and Ungar (2000) stress that another tough pliant food that our early ancestors would have had difficulty processing was meat! They state (2000, p. 13509): “the early hominids were not dentally preadapted to eat meat – they simply did not have the sharp, reciprocally concave shearing blades necessary to retain and cut such foods.”

Both modern chimpanzees and humans have an alimentary track that is neither specialized for eating leaves nor animal protein but instead is more generalized, similar to the majority of primates who are omnivorous and eat a mixture of food types (Chivers and Hladik 1980, 1984; Martin et al. 1985; Martin 1990; Price et al. 2012). Modern humans, especially in Western cultures, think of themselves as meat eaters. For Americans and a whole spectrum of other cultures, meat defines that ephemeral status of wealth and ease for which we strive. Because they, themselves, were rooted in these cultural stereotypes, anthropologists egregiously misnamed the modern forager cultures as hunters and gatherers and initially emphasized only the contributions of male hunters. Nevertheless, more than two-thirds of modern-day foragers’ food comes from women gathering plant foods and, in the process, opportunistically capturing small mammals and reptiles. Less than one-third of the diet (the meat portion brought in through dedicated hunting by men) serves to supplement their foraged nutritional intake, except in cold climates or where fishing is prevalent (Marlowe 2005). Yet, meat can have significance far beyond its mathematical contribution.

Modern dietary concerns in industrial societies revolve around the amounts of both fat and red meat that are consumed by the average person. By the latter portion of the twentieth century, there was a full-blown red alert from the medical community warning that meat should be ingested in limited quantities. “Diseases of affluence” caused by high-protein, high-fat diets include raised cholesterol levels, high blood pressure, heart disease, stroke, breast cancer, colon cancer, and diabetes – all correlated to a diet exorbitantly rich in red meat. With colon cancer, in particular, startling data are available: Daily red-meat eaters are two and one-half times more likely to develop this cancer as are people adhering to a mostly vegetarian diet (Willett et al. 1990). T. Colin Campbell, who compared Chinese rural villagers (eating a traditional diet low in meat) and their urban compatriots (eating more meat), states: “We’re basically a vegetarian species and should be eating a wide variety of plant foods and minimizing our intake of animal foods” (Brody 1990, p. C2). In his Chinese study, Campbell even found that individuals following a low-fat, low-meat diet suffered less anemia and osteoporosis (conditions commonly associated with food *low* in animal products) than individuals higher on the meat-consuming ladder (Campbell and Campbell 2005).

Lastly, no hominins hunted on a large scale before the advent of controlled fire. Again, early humans just did not have the dentition nor the digestive tract of a carnivore. Our anatomy and physiology did not particularly suit us for digesting meat until the mastery of cooking solved the problem. Our intestinal tract is short, and predigestion by fire had to precede any major meat eating (although humans still require certain nutrients that are not obtainable from a meat diet). As stated above, the oldest known hearths with good evidence for controlled use of fire are around 800,000 years old.

Locomotion

By far the best known of early australopithecine species is *A. afarensis*, with many fossil remains dating from between 3.7 and 2.9 mya and possibly as far back as 5 mya. Collections have yielded close to 400 specimens in many East African sites (Kimbel and Delezene 2009). Specimens include the famous Lucy (dated at 3.2 mya), which is the most complete adult skeleton from this time period, and fossil footprints from Laetoli, Tanzania, ash deposits (dated at 3.6 mya). Furthermore, most hypotheses concerning human evolution position *A. afarensis* as a possible pivotal species from which all other later hominins, including *Homo*, evolved (Fleagle 1999; Tattersall 2010; Conroy and Pontzer 2012). Given the above facts, *A. afarensis* is seen as a good species to examine when attempting to reconstruct the appearance and behavior of one of our early human ancestors.

Terrestrial bipedalism is a hallmark of the whole fossil hominin family. This mode of locomotion can be inferred from fossil specimens nearly seven million years old (Galik et al. 2004). It appeared long before the vast growth of open grasslands in Africa and before the expansion of human brain size and recognizable stone tool making. Besides the fossilized bones, direct evidence of early bipedalism comes from the footprints at Laetoli where two hominins were walking together in soft ash almost 4 mya (see Fig. 2) – prints that are remarkably like modern human footprints (White 1980; Tuttle 1985; Day 1985; Feibel et al. 1996). However, looking at the skeletal evidence, the locomotion of these early hominins was not exactly identical to ours. In fact *A. afarensis* seems to have been a primate equally at home in the trees or on the ground indicated by a number of factors. First, the limb proportions are different from anatomically modern humans. The arms are similar in proportion to modern humans, but the legs are relatively much shorter (i.e., more apelike), and this implies the use of suspensory locomotion in the trees (Kimbel et al. 1994). Other aspects of the upper limbs also retain a number of features indicating an ability to move easily in the trees. The wrist and hand bones are quite chimpanzee-like; the finger and toe bones are slender and curved as in apes, giving *A. afarensis* grasping capabilities compatible with suspensory behaviors; the toe bones are relatively longer and more curved than in *Homo sapiens*. The joints of the hands and feet and the overall proportions of the foot bones all reinforce evidence for climbing adaptations and arboreal activity. Nevertheless, the relative thumb length of these hominins is closer to that of modern humans than it is to chimpanzees (Susman et al. 1984; Smith 1995; Corkern 1997; Alba et al. 2003; Conroy and Pontzer 2012).

The pelvis and lower limbs of *A. afarensis* are a mixture of humanlike and apelike features. These anatomical components and the shorter leg length indicate that *A. afarensis* may have used less energy while walking, whereas transition speeds from walking to running may have been lower with slower running speeds

Fig. 2 (*Australopithecines walking at Laetoli*). Reconstruction of two *Australopithecus afarensis*; successes or added advantages of bipedal locomotion were simply by-products of a preadaptation to upright posture (Used by permission of American Museum of Natural History, AMNH Library 4936[2])

than modern longer-legged humans (Steudel-Numbers 2003; but see Conroy and Pontzer 2012). Overall, Rak (1991, p. 283) summarizes: “Although clearly bipedal and highly terrestrial, Lucy evidently achieved this mode of locomotion through a solution of her own.”

A propensity to question the efficiency of primate locomotion is not new to anthropology. It was also once thought that the diminutive Neotropical marmosets and tamarins were restricted in their ability to move on small branches because they have claws instead of the standard primate nails on their hands and feet. However, it has subsequently been proven that claws do not restrict callitrichid locomotion on thin branches; indeed, their claws also enable them to utilize large trunks much like squirrels do. Claws allow them to be more versatile, and they can use a wider range of arboreal habitats than most other new-world monkeys (Garber 1984; Sussman and Kinzey 1984). It appears that the combination of skeletal characteristics found in *A. afarensis* enabled these hominins to be versatile in a similar way. They were able to use the ground and the trees equally and successfully for a very long time. These early hominins were well adapted to their environment and not in the least inhibited by switching back and forth from bipedalism on the ground to quadrupedalism in the trees.

There are at least seven different “models” that have been proposed to account for bipedalism as a hominin adaptive strategy: the *tool using and making* model

(Darwin 1874; Washburn 1960; Sinclair et al. 1986), the *carrying* model (Hewes 1961, 1964; Lovejoy 1981), the *vigilance* model (Dart and Craig 1959; Day 1986), the *heat dissipation* model (Wheeler 1984, 1991), the *energy efficiency* model (Rodman and McHenry 1980; Steudel 1994), the *display* model (Jablonski and Chaplin 1993), and the *foraging* model (Hunt 1994). Each one of the models has some merit, but none of the theories seem to be a strong enough catalyst for switching to a new mode of locomotion. Furthermore, there are many other primates who spend most of their time on the ground, and none of these has developed bipedalism, even though each of the theorized advantages presumably also would have accrued to them.

It is difficult to separate consequence from causation. It cannot be concluded that any of the seven suggested models caused hominins to become bipedal. None of the theories may be causative; instead, all the theoretical "causes" may be results of a primate preadaptation to being bipedal. All the great apes are preadapted to bipedality. When our ancestors came down from the trees, bipedalism was possible because of body proportions and suspensory adaptations – longer arms and shorter legs that allow gibbons, orangutans, and chimpanzees to hang from trees and forage for fruit. All apes have varying capacities for erect posture and are able to walk upright for short periods of time; bonobos, especially, will stride upright with humanlike posture. However, when the earliest hominins began using the ground for a major portion of their activities, their body proportions were more suited for bipedalism than for other forms of locomotion, i.e., quadrupedalism or knuckle-walking. As stated by Fleagle (1999, p. 528):

> Although it is important to see early hominins in the context of hominin evolution, it is equally important to realize that in the same way that they were not little people, they also were not just bipedal chimps, but the beginning of a new radiation of very different hominoids. It is this uniqueness that makes reconstructing hominid origins so difficult. Thus although early hominids and their bipedal adaptations are certainly derived from an African apelike ancestry, human bipedalism is morphologically and physiologically different from the occasional facultative bipedal behaviors occasionally seen in other primates. The morphological and behavioral commitment to bipedalism that characterized early hominids suggests unique ecological and historical circumstances as well.

Some species of primates are intrinsically adapted to edge habitats and, therefore, are able to take advantage of changing environments. It is hypothesized that the earliest hominins were edge species (see below) and that they exploited a terrestrial habitat due to a developing mosaic environment that included climate change. Rather than seeking the factors that *caused* early human ancestors to become bipedal, it is proposed that it was a preadaptation that already existed and it was efficient in a new habitat; the successes or added advantages were simply a by-product. Tattersall (2003) has arrived at a similar conclusion regarding bipedality.

Besides bipedalism and limb use, there are also solid conjectures of what our earliest ancestors were like as far as body build, height, weight, and brain capacity.

From various *A. afarensis* specimens and by examining the skeleton of Lucy, it seems there was a considerable size difference between males and females

(Kimbel and Delezene 2009). Although the canines of both sexes were relatively small and not at all dagger-like, they were larger and longer in the males than in the females. The range of body size for *A. afarensis* individuals is estimated to be 30–45 kg (Fleagle 1999). The height of the adults has been estimated at 1.0–1.7 m (Klein 1999). Lucy stood slightly over 1 m tall and weighed around 30 kg (she was definitely on the small side) (Conroy and Pontzer 2012). If these weights are accurate, we can extrapolate that female *A. afarensis* were the size of male baboons and males were the size of female chimpanzees.

The cranial capacity of these hominins is estimated at 400–500 cm^3 – about the size of a modern chimpanzee but twice as large as Miocene fossil apes. On average, australopithecines and modern chimpanzees have brains that are two to three times larger than similarly sized mammals, whereas modern human brain size is six to seven times larger than other mammals.

Looking at brain size relative to body size, using the encephalization quotient as a measurement, the brain of *A. afarensis* was slightly larger in relation to its body than that of modern chimpanzees ($EQ = 2.4$ for *A. afarensis* versus 2.0 for chimpanzees) (Boaz 1997). Thus, our ancestors were mid- to relatively large-sized primates with brains that were slightly larger than any nonhuman primate, although only a fraction bigger than modern chimpanzees.

There are many speculations about the external appearance of australopithecines. Johanson and Edey (1981) added some details to the portrait of a living Lucy. They pictured her and her kin as small but extremely powerful – their bones were robust for their size, and they were probably heavily muscled. Their arms were longer in proportion to their legs and trunk than modern humans. Their hands were like ours, but their fingers were curled more when in a relaxed position. Heads were more apelike than humanlike with prognathic jaws and no chin. They may have possessed more body hair in comparison to modern humans. While hair color cannot be guessed at from the fossil remains nor can the color of the skin, living in tropical Africa, *A. afarensis* likely possessed darkly pigmented skin with sun-protective melanin (Jablonski 2012).

Habitat of Our Earliest Ancestor

Although many early theories on the evolution of our earliest ancestors stress the importance of arid, savanna environments, these do not seem to be the primary habitats, according to the fossil record, until after 2 mya. The African climate was becoming more arid in the time between 12 and 5 mya, and equatorial forests were undoubtedly shrinking (Segalen et al. 2007; Conroy and Pontzer 2012). However, the process that led to this climatic phenomenon also greatly enlarged areas of transitional zones between forest and adjacent savanna. Closed woodland forests were still widespread in East Africa 3.5 mya, whereas the proportion of dry shrub to grassland habitats began to increase around 1.8 mya (deMenocal and Bloemendal 1995; Shackleton 1995).

It is in these transitional zones that the behavioral and anatomical changes were initiated in early hominin evolution. The flora and fauna remains that are found in association with fossil hominins of this time period indicate a mixed, mosaic environment – mosaic in the sense that it was ecologically diverse and subject to seasonal and yearly changes in vegetation (Potts 1996; Wolpoff 1998; Kimbel and Delezene 2009; Conroy and Pontzer 2012). These environments were wetter than those in which later fossil hominins are found, and most fossil sites of this early time period contained some type of water source, such as rivers and lakes (White et al. 1994; WoldeGabriel et al. 1994, 2001; Reed 1997, 2008; Campisano and Feibel 2007; Wrangham et al. 2009). For example, at Hadar, Ethiopia, the mammalian faunal remains suggest that a lake existed, surrounded by marshy environments fed by rivers flowing off the Ethiopian escarpment; thus, a mosaic of habitats existed at Hadar consisting of closed and open woodland, bushland, and grassland (Reed 2008; Conroy and Pontzer 2012).

The earliest hominins appear to be associated with variegated fringe environments or edges between forest and grassland. These habitats usually contain animal and plant species of both the forest and the grassland, as well as species unique to the borders between the two. The species adapted to these transitional habitats are often referred to as *edge* species or *eurytopic* (i.e., adapted to a wide range of habitats) (Kimbel and Delezene 2009). During these earliest times, it appears that hominins began to take advantage of the growing fringe environments, lessening competition with their sibling ape species which were better adapted to exploit the dense forest and thus partitioning the niche occupied by the parent species of both apes and hominins into two narrower and less overlapping adaptive zones (Klein 1999; LeeThorp et al. 2003; Reed 2008; Conroy and Pontzer 2012). From available evidence it is speculated that our early ancestors were able to exploit a great variety of food resources but were mainly fruit eaters, probably supplementing this diet with some young leaves and other plant parts, social insects, and a small amount of opportunistically captured small vertebrate prey – lizards, small snakes, birds, and mammals. They also likely exploited some freshwater and marine resources (Cunnane and Stewart 2010).

Several other species of primates are intrinsically adapted to edge habitats and are also able to take advantage of changing environments. Ring-tailed lemurs in Madagascar, African baboons, and vervet monkeys, some Asian macaques and langurs, and, to some extent, Neotropical capuchin monkeys are nonhuman primate examples. These, not coincidentally, are some of the most common and numerous of all living primates other than humans. The macaque genus, for example, has the widest geographical distribution of any nonhuman primate in Asia. Many macaque species in Asia are endangered, but the ones that have the healthiest populations (e.g., long-tailed macaques, *Macaca fascicularis*, and rhesus macaques, *M. mulatta*) are edge adapted.

Certain ecological niches may breed certain behavioral repertoires. Many argue that the closer the DNA comparison, the more similar the behaviors between two related species. In that case, chimps and bonobos might be the best prototype for early human ancestors. However, if ecology is paramount, then chimps and bonobos may be less suitable prototypes (although some traits between these close relatives may still be important and phylogenetically conservative) and edge species may be the best models for early humans.

Nearly 40 years ago, Robin Fox (1967, p. 419) declared:

> But the problem of taking the great apes as models lies in the fact of their forest ecologies. Most modern students of primate evolution agree that we should pay close attention to ecology in order to understand the selection pressures at work on the evolving primate lines. This has been shown to be crucial in understanding . . . evolution.

Even if one were to learn everything about the hominin-ape common ancestor, many of the most crucial questions about distinctively hominin evolution would remain unanswered. Although there is a fairly impressive record of human fossils during the period of 7–2 mya, there is a lack of chimpanzee fossils at these early sites. It seems likely, therefore, that chimpanzee ancestors did not inhabit these fringe environments and were likely restricted to more wet, closed forest ecosystems – areas where fossils are less likely to be preserved (Stewart 2010). Some populations of chimpanzees moved into more mosaic, open habitats relatively recently, long after humans had moved into more arid environments. Furthermore, modern chimpanzees do not live in habitats in which modern humans lived in the past or are found today. The historical geographic range of chimpanzees is quite restricted, probably more restricted than even that of early humans before leaving Africa.

To date, the best primate models to use as a basis for extrapolation about behavioral characteristics of our earliest ancestors are modern primate species living in similar edge habitats. Macaques can be extremely good colonizers of edge habitats. The macaque genus spread throughout Asia before humans reached that continent (Delson 1980). By the time *Homo erectus* arrived in Asia 1.8 mya, most hominins were no longer edge species (our more recent ancestors were exploiting more open habitats by this date (Tattersall 2010)), so hominins likely did not displace the macaques. True “weed” species, it is proposed that the macaques are excellent models for reconstructing how our early ancestors may have lived. However, even if macaques are used here, many of the features of the behavior and ecology of these monkeys are very similar to that of other primates living in similar habitats. It is these shared characteristics that make this such a strong model. After all, ultimately, it is the environment in which species find themselves that determines many of their evolutionary adaptations.

The Macaque Model

Long-tailed macaques (*M. fascicularis*) are small edge species that spend a good proportion of time both in the trees and on the ground (see Fig. 3). They are omnivorous and very versatile in their locomotion, although mainly quadrupedal. The most widespread of any Southeast Asian monkey, they occur from Burma through Malaysia and Thailand to Vietnam, while offshore populations are found on Java, Borneo, and numerous smaller islands as far east as the Philippines and Timor. Throughout this area, broadleaf evergreen and other forest types are interspersed with secondary and disturbed habitats, and it is the latter that long-tailed

Fig. 3 (*Long-tailed macaque*). The ecology and social organization of the long-tailed macaque may offer an excellent model of how our early ancestors lived (R. W. Sussman)

macaques prefer. Virtually all of the studies of this species make note that they are most commonly found in secondary forest habitat, preferably near water (Sussman et al. 2011). The success of the long-tailed macaque throughout its extensive Asian distribution is widely credited to its being an "adaptable opportunist" (Mackinnon and Mackinnon 1980, p. 187). Researchers emphasize that these monkeys are extremely adaptable and able to flourish in highly disturbed land.

There is a sizable long-tailed macaque population on the island of Mauritius in the southwest Indian Ocean (Sussman and Tattersall 1981, 1986). Although the original transport of the species from Asia to Mauritius is totally undocumented, it is likely they were onboard the ships when the Portuguese first reached the island and were inadvertently or purposely introduced to the primate-deficient ecosystem. Cited from the first studies as an assertive colonizer of new habitat, the small number of original immigrants had increased to 40,000 animals (before recent exportation of macaques for medical research) – successfully living up to their reputation as colonizers of disturbed and varied habitats (Sussman and Tattersall 1986; Sussman et al. 2011).

Long-tailed macaques are slender, active monkeys; average weight is 4–5 kg for females and 6–7.75 kg for males (Jamieson 1998). Long-tailed macaque society is organized around matrilineal hierarchies. There are always one or two dominant males visible within the group, as well as some lower-ranking adult males, plus the adolescent and subadult male offspring of the females. At sexual maturity males migrate to a new group. Female offspring are philopatric, mating with unrelated males who join their troop (Jamieson 1998).

Many of the Man the Hunter models ignore or minimize the role of females in human evolution. In many terrestrial and edge-adapted nonhuman primate species, such as long-tailed macaques and baboons, females are the core of society, remaining with their female relatives from birth to old age. Each matriline consists of several generations and can be placed in a dominance hierarchy. Highly social females inherit the rank of their mothers, so the troop organization remains relatively stable over time.

Man the Hunter scenarios typically depict male hunters as leaders, innovators, tool makers, and tool users. Since these aspects of gender specificity may never be revealed in the fossil record, it may be justifiable to construct theories based on the behavior of our primate relatives. When Japanese macaques were first studied in the wild, it was the young females who started innovative behaviors such as new ways of processing food (Kawai 1958). Chimpanzee tools are made primarily by females and used mainly in gathering activities such as nut cracking and termite fishing; it is also the female chimpanzees who teach the next generation how to use these tools (Boesch and Boesch-Achermann 2000; Sanz 2004). Furthermore, in most primates, females are the repositories of group knowledge concerning home ranges and scarce resources. Group knowledge and traditions are passed on from mother to offspring, and stability of the group, both in the present and over time, is often accomplished through female associations (Zihlman 1997).

In most primates adapted to edge environments, it is the males who migrate. However, in the closest genetic relatives of humans, the gorillas, chimpanzees, and bonobos, females normally change groups when they mature. This appears to be a phylogenetically conservative characteristic among hominoids which makes it possible that among our earliest ancestors, females, not males, migrated between groups. However, most modern human foragers are multilocal, with individuals residing with their maternal relatives at times and with their paternal relatives at other times or sometimes with neither (Marlowe 2005).

The ability of edge species to exploit a wide variety of environments is accompanied by a substantial flexibility of behavior. Long-tailed macaques appear to be primarily arboreal where suitable vegetation exists, but they come to the ground along riverbanks, seashores, and in open areas – and in some portions of their recently colonized range, such as Mauritius, they are highly terrestrial (Sussman and Tattersall 1981). They are eclectic omnivores with a distinct preference for fruit. But the variety of habitat they exploit is reflected in a wide selection of food items – besides fruit, they feed on leaves, grasses, seeds, flowers, buds, shoots, mushrooms, water plants, gum, sap, bark, insects, snails, shellfish, bird eggs, and small vertebrates (Sussman and Tattersall 1981; Yeager 1996; Sussman et al. 2011). Human-disturbed habitat or proximity to human settlements is not avoided; rather, they tend to live commensally with humans throughout their range, which results in crop raiding of sugar cane, rice, cassava, and taro fields.

Long-tailed macaques live in large multi-male, multi-female groups of up to 80 individuals, although in some areas groups are much smaller. They show distinct flexibility in structure; the large basic social unit tends to split up into smaller subgroups for daytime foraging activities (Jamieson 1998; Sussman et al. 2011). Subgroups may be all males, but most often consist of adult males accompanying females and their young offspring. The number and size of subgroups tend to vary with the season and resource availability (Jamieson 1998). The entire troop reforms each evening and returns to the same sleeping site each night, usually on the edge of a water source. Because of their unique behavior of returning to a home base each night, long-tailed macaques have been labeled a "refuging" species.

Fossils and Living Primates

Looking at the fossil evidence, it is apparent that human ancestors, living between 7 and 2.5 mya, were intermediate-sized primates, not smaller than male baboons or larger than female chimpanzees. Given their relative brain size, they were at least as clever as the great apes of today. They had diverse locomotor abilities, exploiting both terrestrial and arboreal habitats. They used climbing and suspensory postures when traveling in the trees and were bipedal when on the ground. It is believed that their bipedalism was a preadaptation, but walking on two feet freed the arms and hands and proved to be advantageous in a number of ways.

Given their relatively small size and small canines, there is no reason to think that our early ancestors were any *less* vulnerable to predation than are modern monkeys – some of which have yearly predation rates generally comparable to gazelles, antelopes, or deer living in similar environments (Hart 2000; Hart and Sussman 2009). Indeed, edge species can be *highly* vulnerable to predation and because of this usually live in relatively large social groups with many adult males and adult females; adult males often serve as sentinels and provide protection against predators (Hart and Sussman 2009). Because a primate group with only one male and ten females can have the same reproductive output as a group with ten males and ten females, often the male role in primate groups is to act as a first line of defense. If he gets eaten there are other males to take his place, but if a sexually mature female gets eaten, then she and all her potential offspring (and living dependent infants) are lost.

Like long-tailed macaques, our human ancestors may have lived in multi-male, multi-female groups of variable size that were able to split up depending on the availability of food and reform each evening at home base refuges. However, certain facts such as the exact size of the groups and subgroups, whether males or females migrated from the group when they reached sexual maturity, and the internal structure of the group (whether matrilineal or formed along male kinship lines) would be impossible to determine accurately. Indications of these social parameters cannot be found in the fossil record and are quite variable even in closely related living primates.

In sum, the best archetype of early humans may be a multi-male, group-living, mid-sized, omnivorous, quite vulnerable creature living in an edge habitat near a large water source. These hominins may well have been a refuging species returning to the same well-protected sleeping site each night. (Most modern foragers are considered central place foragers, focusing their activities around a principal location, as are many birds, social carnivores, and primates (Marlowe 2005).) These creatures were adept at using both the trees and the ground, but when they exploited the terrestrial niche, they had upright posture and were bipedal. They depended mainly on fruit, including both soft fruits and some that were quite brittle or hard, but also ate herbs, grasses, and seeds and gritty foods such as roots, rhizomes, and tubers. A very small proportion of their diet was made up of animal protein, mainly social insects (ants and termites) and, occasionally, small vertebrates captured opportunistically. These early humans did not regularly hunt for meat and could neither process it dentally nor in their digestive tracts.

Like all other primates and especially ground-living and edge species, these early humans were very vulnerable to predators, and this trait did not diminish greatly over time (Hart and Sussman 2009). Fossil evidence to this effect exists from Ethiopia and South Africa, from the Zhoukoudian cave in China, from European sites such as the skulls uncovered at Dmanisi in the Republic of Georgia, and from Olorgesailie and Tugen Hills, Kenya (see Table 1).

Man the Hunted

Given that the earliest hominin ancestors were medium-sized primates who did not have any inherent weapons to fight off the many predators that lived at that time – and given that they lived in edge environments which incorporate open areas and wooded forests near rivers – then, like other primates, they were vulnerable to predation. Because of this it is hypothesized that rates of predation were just as high in our early ancestors as they are in modern species of primates and that our origins are those of a *hunted* species (Hart and Sussman 2009) (see Fig. 4).

Protection from predation is one of the most important aspects of group living, and it is believed this was true of our earliest ancestors. Based on the long-tailed macaque model, social groups of early hominins may have been organized in a way that allowed efficient exploitation of a highly variable and changing environment and also protected its members of the group from predators. If the human lineage started out as Man the Hunted, it is proposed that a number of strategies for protection from predators are based on the behavior and social organization we observe in long-tailed macaques.

- Relatively large groups of 25–75 individuals: Since safety lies in numbers, one of the main reasons all diurnal primates live in groups is predator protection which provides more eyes and ears alert to presence of predators as a first line of defense. In his research on modern human foragers, Marlowe (2005) found that the median group size is 30 individuals.

Table 1 Hominin fossils

Fossil	Site	Approximate age	Evidence	Assumed predator	References
Orrorin tugenensis	Tugen Hills, Kenya	6 mya	Tooth marks on several bones	Leopard-like carnivore	Senut 2001
Ardipithecus ramidus	Aramis, Ethiopia	4.4 mya	Tooth marks on cranial and postcranial elements	Carnivore	WoldeGabriel et al. 1994
Australopithecus africanus	Taung Quarry, South Africa	2.5 mya	Punctures and incisions at base of eye sockets; talon rakings on cranium	Extinct raptor (*Stephanoaetus* spp.)	Berger and Clarke 1995; McGraw et al. 2006
Homo erectus	Dmanisi, Rep. of Georgia	1.8–1.7 mya	Canine tooth indentations on cranium; gnaw marks on mandible	Saber-toothed cat	Gabunia et al. 2000; Gore 2002; Wong 2003
Paranthropus robustus	Swartkrans, South Africa	1.8–1.5 mya	Canine tooth indentations at base of cranium	Fossil leopard (*Panthera* spp.)	Brain 1981
Homo?	Orce, Spain	1.6 mya	Cranium fragment excavated from fossil hyena den	Short-faced hyena (*Pachycrocuta brevirostris*)	Borja et al. 1997
Homo?	Olorgesailie, Kenya	900,000 ya	Bitemarks on the left browridge	Carnivore	Fox 2004; Small 2005
Homo erectus	Zhoukoudian, China	450,000 ya	Crushing of facial bones, maxilla, and mandible; enlargement of foramen magnum	Short-faced hyena (*Pachycrocuta brevirostris*)	Boaz et al. 2000; Boaz and Ciochon 2001; Boaz et al. 2004
Archaic *Homo sapiens* (*"helmei"*)	Florisbad, South Africa	260,000 ya	Canine tooth depression on forehead	Hyena	Deacon and Deacon 1999
Homo neanderthalensis	Mt. Cicero, Italy	50,000 ya	Fractures on cranium; enlargement of foramen magnum; gnaw marks on mandible	Hyena	Bahn 2005

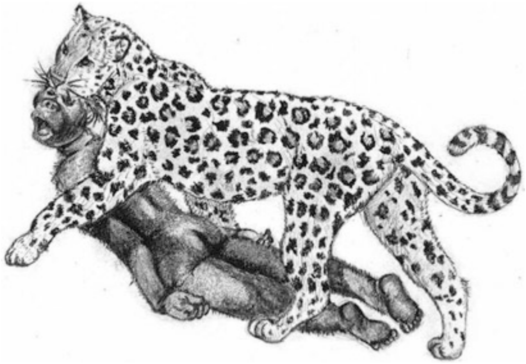

Fig. 4 (*Leopard capturing australopithecine*). Fossil evidence from South Africa documents predation by leopards on our early ancestors (C. Rudloff, redrawn from Brain 1981)

- Versatile locomotion that exploits both arboreal and terrestrial milieus: The major advantage of agility in the use of diverse habitats is safety in trees and dense underbrush. An added advantage of upright posture is the ability to scan for predators.
- Flexible social organization: For example, gathering scarce resources in small groups but reuniting as a larger group when predation requires strength in numbers allows small groups to quickly disperse and hide while large groups can mob and intimidate predators. Again, modern human foragers fit this pattern of flexibility (Marlowe 2005).
- Multi-male social structure: This demographic feature provides more male protection both when traveling through open areas and when the group settles in evening or midday. When large groups break into subgroups, females and young are accompanied by one or more large males.
- Males as sentinels: Males are usually larger in these species. Upright posture adds to the appearance of large size and also allows for better vigilance, as well as waving arms, brandishing sticks, and throwing stones. Males mob or attack predators since they are the more expendable sex.
- Careful selection of sleeping sites: Refuging species bring the whole group together at night in a safe area. During daytime rest periods, staying in very dense vegetation is essential. Males should stay on high alert during these inactive periods and when the group is on the move.
- Stay one step ahead of predators: Intelligence endows primates with the ability to monitor the environment, communicate with other group members, and implement effective anti-predator defenses (Hart and Sussman 2009).

Reconstruction of the behavior and ecology of our earliest hominin ancestor reflects the pervasive influence of large ferocious predatory animals throughout human evolution. Many circumstances have been proposed as a catalyst for the evolution of the human species – competition for resources, intellectual capacity, male-male conflicts, and hunting. But looking at our primate relatives and the fossil record, it is believed that predation pressure was one of the most critical components in shaping the evolution of our earliest ancestors.

Conclusion

While many models have been developed to depict the behavior and ecology of our earliest relatives, the Man the Hunter model has been the most widely accepted view of human evolution. Many human traits, such as bipedalism, tools, and fire, are often linked to this Man the Hunter perspective. Theories of human aggressive hunters abound but are rarely based on evidentiary approaches. Here, using a methodology based on the fossil record and extant primate ecology and behavior, data on fossil humans, on modern primates, and on rates of predation indicate that Man the Hunted may be the most accurate descriptor of our earliest relatives.

Cross-References

▶ Cooperation, Coalition, Alliances
▶ Dental Adaptations of African Apes
▶ Estimation of Basic Life History Data of Fossil Hominoids
▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
▶ Geological Background of Early Hominid Sites in Africa
▶ Great Ape Social Systems
▶ Historical Overview of Paleoanthropological Research
▶ Hominin Paleodiets: The Contribution of Stable Isotopes
▶ Modeling the Past: The Paleoethnological Approach
▶ Origin of Bipedal Locomotion
▶ Origin of Modern Humans
▶ Postcranial and Locomotor Adaptations of Hominoids
▶ Primate Intelligence
▶ Role of Environmental Stimuli in Hominid Origins
▶ The Biotic Environments of the Late Miocene Hominoids
▶ The Hunting Behavior and Carnivory of Wild Chimpanzees
▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
▶ The Paleodemography of Extinct Hominin Populations
▶ The Species and Diversity of Australopiths

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Modeling the Past: The Paleoethnological Approach

Paolo Biagi

Contents

Abstract

This chapter considers the earliest Paleolithic, Oldowan (Mode 1), and Acheulean (Mode 2) cultures of the Old Continent and the traces left by the earliest hominids since their departure from Africa. According to the most recent archaeological data, they seem to have followed two main dispersal routes across the Arabian Peninsula toward the Levant, to the north, and the Indian subcontinent, to the east. According to recent discoveries at Dmanisi in the Caucasus, the first Paleolithic settlement of Europe is dated to some 1.75 Myr ago, which indicates that the first "out of Africa" took place at least slightly before this date. The data available for Western Europe show that the first Paleolithic sites can be attributed to the period slightly before 1.0 Myr ago. The first well-defined "structural remains" so far discovered in Europe are those of Isernia La Pineta in Southern Italy, where a semicircular artificial platform

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P. Biagi (✉)
Department of Asian and North African Studies, Ca' Foscari University – Venice, Venezia, Italy
e-mail: pavelius@unive.it; paolo.biagi@unive.it

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made of stone boulders and animal bones has been excavated. The first hand-thrown hunting weapons come from the site of Schöningen in north Germany, where the first occurrence of wooden spears, more than 2 m long, has been recorded from a site attributed to some 0.37 Myr ago. Slightly later began the regular control of fire. Although most of the archaeological finds of these ages consist of chipped stone artifacts, indications of art seem to be already present in the Acheulean of Africa and the Indian subcontinent.

Introduction

The aim of this chapter is to review the current evidence for the paleoethnology of the early hominids who inhabited the Old World from the time of their appearance up to the end of the Middle Pleistocene. Although the data presently available are not abundant, there is no doubt that they are of key importance for the understanding of early hominid behavior and lifestyles. The evidence is limited in most cases to stone tools and their contexts (Clark 1968, p. 277), almost exclusively due to natural and environmental factors both *physical and biological* (Stiles 1998, p. 134; McNabb 2009).

Given that the term paleoethnology rarely occurs in the Anglo-Saxon literature, while it is, or better was, more common in several European countries, it may be useful to review the meaning of this term and how it originated. It derives from the Greek palaiòs èthnos lògos (study of ancient populations) and was first used in France around the middle of the nineteenth century, and immediately afterward in Italy when prehistoric studies began to flourish, mainly in the Po Valley region of Emilia. The term paleoethnology (Pigorini 1866; Regazzoni 1885) was formally adopted during a congress exclusively devoted to the new science (“scienza nuova”) held in La Spezia on September 20, 1865, by the Italian Society of Natural Sciences (Tarantini 2012, p. 30). At this meeting, the French engineer Gabriel de Mortillet proposed the foundation of an International Paleoethnological Congress that was enthusiastically accepted by all delegates. A few years later, in 1875, Luigi Pigorini (Guidi 1987), Gaetano Chierici (Magnani 2007), and Pellegrino von Strobel (von Strobel 1998) founded a new journal in Parma, “Bullettino di Paletnologia Italiana,” the first to exclusively deal with prehistoric archaeology”.

In those years, the term paleoethnology was preferred to that of prehistoric archaeology because it was more strictly connected with the ethnographic discoveries under way in the Americas, Africa, and Asia (Figuier 1870, p. 415; Lubbock 1870) and favored analogy studies (Hodder 1982, p. 12) between the prehistoric finds recovered from excavations in European prehistoric sites and those still in use among the native communities of the above continents (Desittere 1988). In this respect, it is important to remark that even Boucher de Perthes (1864), the famous discoverer of Abbeville and the first Early Paleolithic hand axes in continental Europe (Prestwich 1860; Lamdin-Whymark 2009, p. 49), had a collection of flint tools from not only Europe but also Asia and Africa (Gowlett 2009, p. 18). This is the reason why paleoethnology courses are still delivered in the Italian university, due to the long tradition that goes back to the earliest prehistoric studies of the mid-nineteenth century.

Reverting to the early stone tool assemblages of the first hominids, they are often associated with alluvial sedimentary processes (Isaac 1967) related to the geographic and geomorphologic location and distribution of the (sometimes ephemeral) sites (Brown 1997, p. 150) that in many cases are limited to the stone tools themselves and possibly to organogenic tools and the faunal remains derived from hunting and scavenging activities (Conard 2007). Nevertheless, the excavations carried out during the last 50 years, and the study of the settlement structures and tool assemblages of the Early Paleolithic sites of the Old World, "have shown that it is quite possible to find sealed occupation sites that have suffered little or no natural disturbance before or after burial" (Clark 1968, p. 276).

As far as the remains of material culture and their chronotypological characteristics are concerned, this chapter deals almost exclusively with Mode 1 (Oldowan) and Mode 2 (Acheulean) complexes (Clark 1994; Toth and Schick 2007). Tools belonging to these two "modes" have been collected from a great number of sites, which are distributed between East Africa and the Indian subcontinent in the southeast and Europe in the northwest (Movius 1948, p. 409; Otte 2000, p. 111).

Out of Africa

Much has been published dealing with the spread of the first hominids and the radiometric dating(s) of the "out of Africa" dispersal(s) (Chauhan 2005; Petraglia 2007; Rightmire 2007). Nevertheless, many questions are still unresolved, since "the triggers for the movement of humans out of Africa are not well known" (Bar-Yosef and Belfer-Cohen 2000, p. 81). Stone tool technotypological variability, between Africa and Asia, for instance, would suggest a series of cultural complexities (Braun et al. 2010). The chronology is also very variable and badly known, in India for instance (see Chauhan 2010 contra Gaillard et al. 2010). This state of affairs results from the absence or scarcity of reliable data from some of the key territories that hominids must undoubtedly have crossed to reach Eurasia (see, for instance, Petraglia 2003, Fig. 12).

This is the case for Arabia, from which little information is currently available, especially from the southern portions of the peninsula, more precisely Yemen (Dhofar) and Oman, which were most probably reached by the Afar Depression across the dried Red Sea strait (Cachel and Harris 2007, p. 120). Effectively, the Early Paleolithic sites discovered in these countries come from a few, restricted areas where intensive surveys and excavations have been carried out in the last two decades (Whalen and Pease 1991; Cremaschi and Negrino 2002; Whalen et al. 2002; Whalen and Fritz 2004; Amirkhanov 2006). Even though many of them are represented by surface finds, the Soviet-Yemeni Archeological Mission excavated thick sequences in some caves of southeast Yemen, close to the Dhofar border. This led to the discovery of stratified complexes, which Amirkhanov (1994, p. 218) attributed to the pre-Acheulean (Oldowan: Mode 1) and Acheulean (Mode 2) periods. In this context, the only tool bearing evident traces of use, from the lowermost layers of Al-Guza Cave in Yemen (Amirkhanov 2006, p. 91), is of unique importance. This is the only pre-Acheulean worn chopper so far known from the entire south Arabian Peninsula.

Although the Early Paleolithic sites so far discovered in this region are few, south Arabia is claimed to represent one of the key routes followed by the first hominids once they started to move out of Africa, initially moving along the coast of the peninsula, to reach its interior slightly later (Rose and Petraglia 2009, p. 6), moving to the central territories of the Indian subcontinent, undoubtedly earlier than 1.0 Myr ago (Bar-Yosef and Belfer-Cohen 2000, p. 82). A second route is said to have been followed "across the Sinai into western Asia . . . although this has not been adequately detailed to date" (Bar-Yosef 1994, p. 237; Petraglia 2003, pp. 168–169), where the oldest site known to date is located at 'Ubeidiya (Stekelis et al. 1969; Bar-Yosef 1995, p. 250) (Fig. 1).

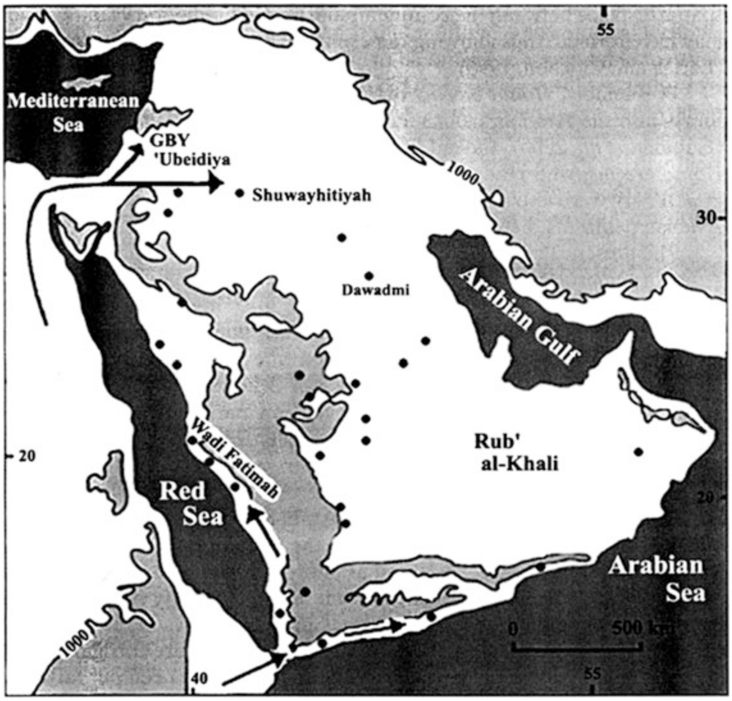

Fig. 1 The Arabian Peninsula with the indication of the most important Early Paleolithic sites (*dots*) and the potential main routes followed by hominids during their "out of Africa" dispersal (s) (*arrows*) (After Petraglia 2003, Fig. 12)

Important radiometric dates for the first human dispersal are available from Dmanisi (Fig. 2) in the Georgian Caucasus (Gabunia et al. 1999; Nioradze and Nioradze 2011). The excavations carried out at this site over a surface of some 300 m^2 led to the discovery of a unique settlement with skeletal remains of early hominids, identified as *Homo ergaster* (Lordkipanidze and Vekua 2006), among which are five skulls, over 10,000 chipped stones obtained from different raw materials (for instance, mostly available close to the site as river pebbles), mainly represented by choppers and flakes, and over 7,000 animal bones, belonging to a faunal assemblage of "Villafranchian type." They undoubtedly show that this dispersal took place not later than 1.8 Myr ago (Gabunia 2000, p. 43; Vekua et al. 2011). Nevertheless, "le mouvement oriental paraît à la fois beaucoup plus complexe et, surtout, beaucoup plus ancien qu'en Europe" (Otte 2000, p. 108). Fortunately, the number of discoveries of Lower Pleistocene sites from this continent is systematically increasing (de Lumley 1976; Agustí et al. 2000; Mussi 2001, p. 20). Although the absolute age of some of these sites is problematic (Santonja and Villa 1990, p. 54), many are undoubtedly much older than supposed only a few years ago (Roebroeks and van Kolfschoten 1994, p. 500). Although the number of radiometric dates currently available from southern Europe is very limited, nevertheless they show that at least some north Mediterranean regions were undoubtedly settled by hominids as early as 1.3 Myr ago (see, e.g., de Lumley et al. 1988; Peretto et al. 1999; Toro-Moyano et al. 2003) as suggested by recent discoveries made at Pirro Nord, in southeastern Italy (Arzarello et al. 2007, 2012).

Fig. 2 Dmanisi (Georgia): A view of the hominid archaeological site with the Medieval pit (*on the right*) from which the first prehistoric bones were discovered (Photograph by P. Biagi)

Chipped Stone Assemblages

Bifaces and Other Tools

As pointed out by Gowlett (2005, p. 51), “East Africa is the key territory for examining the Oldowan and early Acheulean,” in which the first “bifacial tools were created about 1.5 million years ago” (Porr 2005, p. 68) by *Homo ergaster*, as a consequence of a complex series of behavioral, economic, and social factors whose complexity has been pointed out by Porr (2005, p. 77). Until recently, however, they have been considered almost exclusively in the context of “artefacts as a functional form that varies sometimes according to raw material considerations and is manufactured with a recurrent technology within broader parameters” (Ashton and McNabb 1993, p. 190). But the fact that the manufacture of such tools continued for some 1.25 Myr indicates their importance, most probably not only as cutting and/or scavenging weapons (Domínguez-Rodrigo 2002) but also as social indicators independent of their functional meaning(s). According to Draper (1985, p. 7), “we could imagine a situation where an Early Paleolithic hominid might have fabricated a portable cutting tool for scavenging remnant meat from carnivore kills” that “was produced because a Middle Pleistocene knapper . . . was disposed to work stone in a way that produced an object we call a handaxe” (Hopkinson and White 2005, p. 21). The high variability (Sinclair and McNabb 2005, p. 185), the typological and dimensional characteristics (Isaac 1977), their eventual hafting (Ling 2011), and the “wide temporal and geographic distribution” (Wynn 1995, p. 11) of these tools have been noted by many authors, but from different perspectives and with different aims (Bordes 1968, p. 23; Camps 1979; Petraglia 1998, p. 371; McNabb et al. 2004; Hopkinson and White 2005) (Figs. 3 and 4). In Asia, their distribution covers a well-defined region, delimited in the east and the north by the so-called Movius Line (Movius 1944, p. 103), more of a “veil” than a real line according to Otte (2010, p. 274). This “line” is still nowadays often employed to mark the limit between hand axe and other technologies with no evidence of bifacial tools, like the Soanian of northern Pakistan (De Terra and Paterson 1939; Paterson and Drummond 1962), though bifacial tools are recorded from its more recent period of development (Graziosi 1964, p. 12), or the Anyathian of Burma (De Terra and Movius 1943) to make two well-known examples often referred to very different chronological periods of the Paleolithic. In this respect, the discovery of undated bifacial forms in Australia is intriguing and might possibly help clarify some aspects of their manufacture, meaning, and function (Brumm and Rainey 2011).

Although the complexity involved in the production of the lithic artifacts has been openly questioned (Hassan 1988, p. 281), and analysis of manufacturing techniques and debitage dispersal (Andrefsky 2007) across the earliest Paleolithic sites (Gowlett 2005; Petraglia et al. 2005) is still rarely applied by the field archaeologists, a few interesting exceptions should be mentioned. Among these is the MNK chert factory site in the Olduvai Gorge (Tanzania), which is dated to some 1.6 Myr ago. Here chipped stone artifacts, obtained from both local and imported raw materials, show a complex sequence of activities carried out by “early man working a raw material

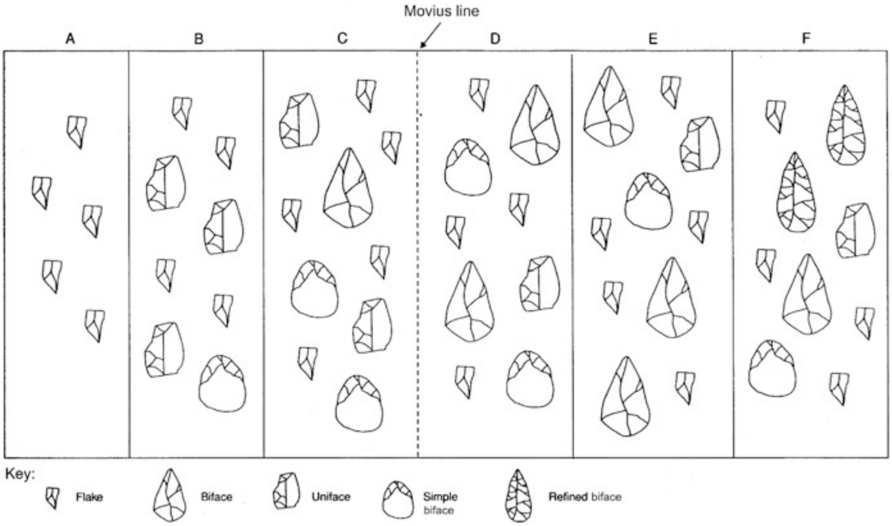

Fig. 3 Variation among lower Paleolithic biface assemblages of Eastern Asia and South Asia. The *dashed line* represents the Movius Line, the traditional demarcation between Mode 1 (Oldowan) and Mode 2 (Acheulean) industries (After Petraglia 1998, Fig. 11.8)

chosen for its technological properties brought to a central locality from diverse sources" (Stiles et al. 1974). FxJi50, in north Kenya, is a site 1.5 Myr old that "consists of a patch of stone artefacts interspersed with broken-up fragments of bone" (Bunn et al. 1980, p. 111), whose precise function is still difficult to define. The chipped stone assemblage, which is composed of flaked cobbles and flakes partly obtained on the spot, "has proved to consist of several dense clusters of material that interconnect with each other" (Bunn et al. 1980, p. 114). This is one of the earliest Paleolithic sites from which "the close association (of bones) with artefacts and the presence of butchering marks suggest that the toolmakers were the first accumulating agency" (Bunn et al. 1980, p. 125). This picture is rather unusual, if we consider that "for most of the sites excavated and reported we do not have certain indications of any specific activities that characterize them, and in very few instances has localization of subsidiary tool kits within a floor even been claimed" (Isaac 1972, p. 185) and that the interpretation of the variability of the spatial distribution pattern of the tools (Whallon 1973, p. 117) within a site surface is often difficult (Keeley 1991, p. 258). Experimental studies have also been made especially regarding hand-axe production employing different techniques and raw materials and using both hard and soft hammerstones (Madsen and Goren-Inbar 2004).

Raw Material, Workshops, and Quarries

When detailed recording methods have been applied, as for instance in the case of some localities excavated in the Indian subcontinent, they have revealed that

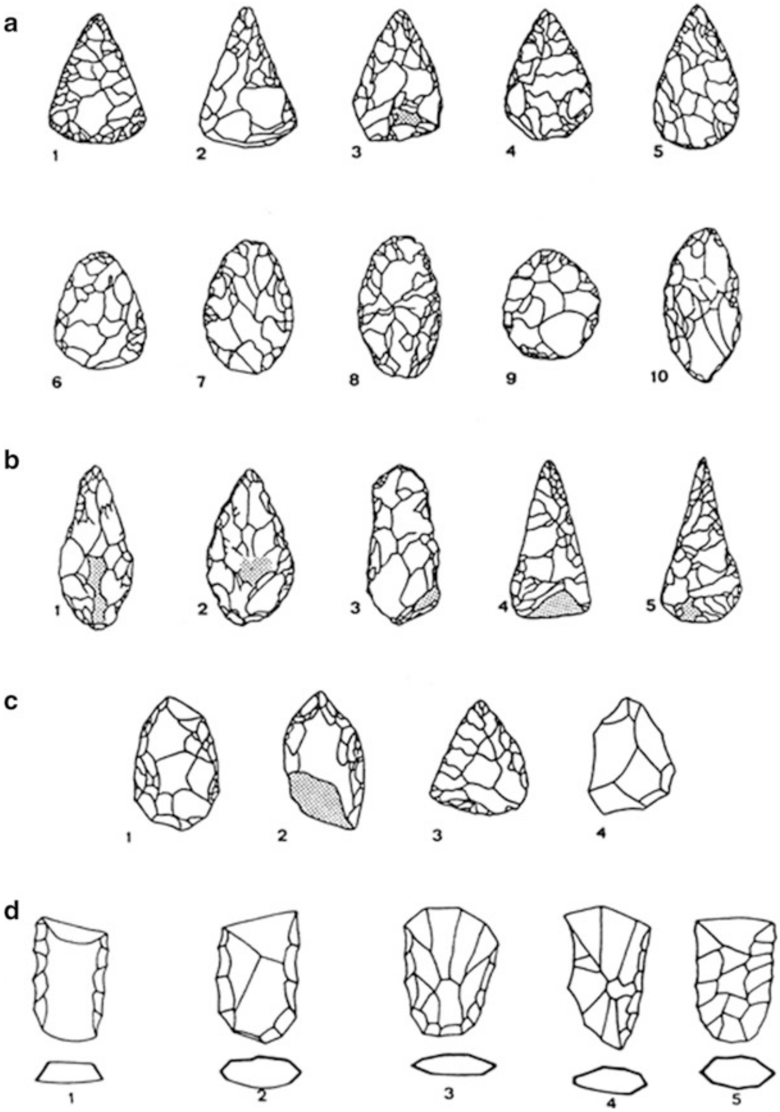

Fig. 4 Different categories of hand axes according to the typological classification proposed by Camps (1979): different types of (**a**) flat bifacials, (**b**) thick bifacials, (**c**) diverse bifacials, and (**d**) *hachereaux* (After Broglio 1998, Fig. 22)

characteristic tools, among them hand axes, cores, hammerstones, and different dimensional classes of debitage flakes, systematically cluster in well-defined spots (see Pappu 2001, pp. 25–54; Paddayya et al. 2002, p. 646). This fact is useful in helping us understand the development of the manufacturing areas within the site and the steps followed by the toolmakers during the production process

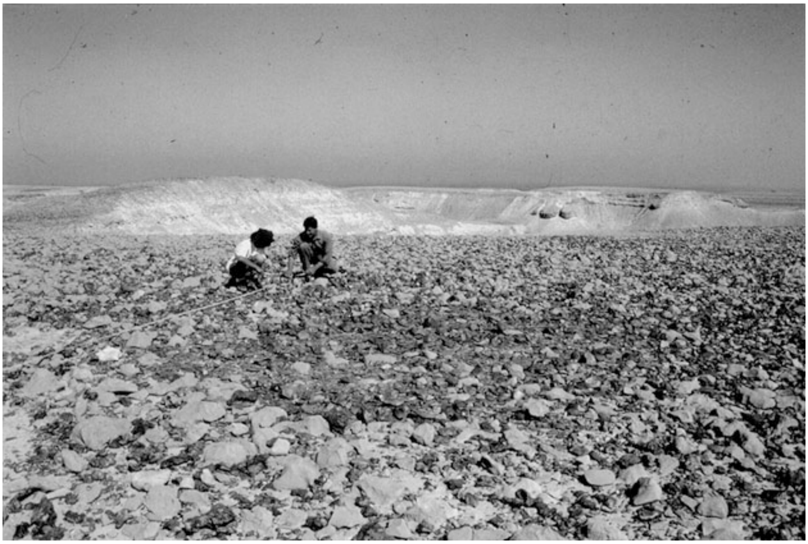

Fig. 5 Ziarāt Pir Shabān on the Rohri Hills (Sindh, Pakistan): The Acheulean hand-axe factory ZPS1 before excavation (Photograph by P. Biagi)

(Hansen and Madsen 1983, p. 51), especially when refitting methods are applied to the entire complex (Bergman et al. 1990, p. 280). This is the case for the some Acheulean sites where different varieties of raw materials for tool production were available, including siliceous limestone (Isampur in India: Petraglia et al. 2005) and good-quality chert from local outcrops (Rohri Hills in Sindh [Pakistan]: Biagi et al. 1996).

The evidence available from the latter shows that the waste products of large hand-axe-manufacturing workshops were scattered along the edges of circular sandy areas representing zones that were comprehensively cleared of limestone and chert boulders in Paleolithic times, before the manufacturing activities took place. For instance, the excavations carried out at Ziarāt Pir Shabān 1 (Fig. 5), one of the many Acheulean workshops discovered on the Rohri Hills that were exclusively devoted to the production of hand axes (Biagi et al. 1996) (Fig. 6), have demonstrated that the perfect, finished bifaces were exclusively transported elsewhere, most probably to camps located in the adjacent Great Indian Desert that are at present buried beneath meters of sand inside thick, stabilized dunes (Misra and Rajaguru 1989). The maximum transfer distance is not known, due to the absence of any detailed research in the Thar Desert to the east of the hills, although the African parallels indicate transport between 15 and 100 km (Petraglia et al. 2005, p. 208). A situation similar to that of the Rohri Hills is known at Ongar, near Hyderabad in lower Sindh (Pakistan), where Acheulean workshops were discovered lying on the top of flat limestone mesas (Figs. 7 and 8). These deposits, very rich in seams of excellent chert, were exploited throughout the entire Paleolithic period, from the Acheulean onward (Biagi 2006, 2008).

Fig. 6 Ziarāt Pir Shabān on the Rohri Hills (Sindh, Pakistan): Acheulean hand-axe rough-outs on the surface of workshop ZPS1 (Photograph by P. Biagi)

Fig. 7 Ongar (Sindh, Pakistan): C-shaped Acheulean chert factory area (Photograph by P. Biagi)

As far as these two latter cases in Sindh are concerned, there is no doubt that the abundance of excellent, workable raw material played a fundamental role in attracting prehistoric populations at least since the Acheulean period (Biagi and Cremaschi 1988, p. 425). The chert used by the earliest Paleolithic people was

Fig. 8 Ongar (Sindh, Pakistan): In situ chert flakes concentration in an Acheulean workshop (Photograph by P. Biagi)

collected from large boulders or extracted from the top of the limestone terraces, as supported by the evidence from accurate surveys carried out along the top of the mesas that did not reveal any trace of Early Paleolithic mining activities.

As far as we know, the first Paleolithic chert quarries were opened by Acheulean populations, both in the Levant (Gopher and Barkai 2011) and Upper Egypt, much earlier than until recently supposed (Smolla 1987, p. 129). According to Vermeersch et al. (1995, p. 22), "a few kilometres south of the Dandara temple …a… hill was clearly subjected to chert extraction by Acheulian people," given the presence of an extractive pit discovered during the excavation of a small trench in an area rich in Late Acheulean tools. In contrast, almost nothing is known of Acheulean raw material procurement systems in this region, which yielded abundant traces of Middle and Upper Paleolithic flint-mining activities (Vermeersch et al 1997, p. 191).

Habitation and Other Structural Remains

Early Paleolithic Mode 1 and 2 sites are often characterized by "concentrations of debris, … which… have usually been interpreted to be the result of various processual phenomena" (Stiles 1998, p. 133). Only a few of them, of varied chronology, have provided us with complex archaeological evidence (see, e.g., Pappu 2001).

In Africa, we know that most of the earliest settlements were located in environments close to lake shores or, more commonly, along (former) river courses

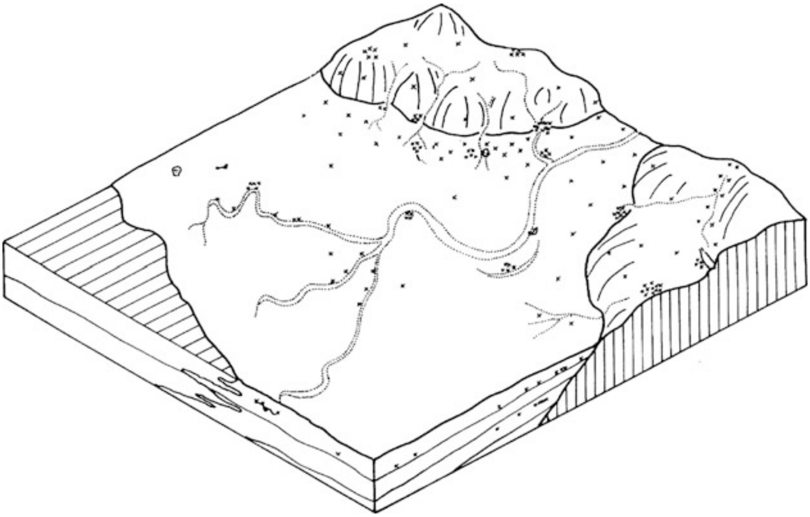

Fig. 9 Schematic representation of a portion of landscape frequented by tool-using hominids, with the locus of discarded artifacts marked X (After Isaac 1976, Fig. 3.3)

(Isaac 1976, Fig. 3.3) (Fig. 9). They have been interpreted as sites that are inhabited during only one season, whose remaining components, mainly lithic artifacts and bones, show they had been planned (Binford 1989a, p. 469). The 1.75-Myr-old Mode 1 site of DK, in Lower Bed I of the Olduvai Gorge (Leakey 1971, p. 24, Fig. 7), yielded evident traces of man-made features, the most important of which consists of a circular structure of lava blocks, some 4.5 m in diameter (Fig.10), that the excavator interpreted as resembling "temporary structures often made by present-day nomadic peoples who build a low stone wall round their dwellings to serve either as windbreak or as a base to support upright branches which are over and covered with either skin or grass" (Leakey 1971, p. 24).

The excavations carried out at Gomboré I, another Mode 1 site located at Melka Konturé in Ethiopia, brought to light a 230 m^2 living floor composed of rounded pebbles and rich in stone tools and faunal remains, with a central empty space of some 10 m^2. The settlement, which has been dated at some 1.6 Myr ago, yielded a "higher platform . . . that . . . could have been roughly adapted for a shelter made of branches and animal skins" (Chavaillon 2004, p. 263). The research carried out at this site revealed the occurrence of "small stone circles aligned north-south in the eastern sector . . . whose . . . external diameter . . . varies from 20 to 40 cm," which were interpreted as possible "wedging stones for pegs set in rather hard soil" (Chavaillon and Chavaillon 2004, p. 448), similar to those recorded from Garba XII in the same region. Recent radiometric dates obtained from a few Early Paleolithic localities in the area revealed a sequence of habitation covering a long period comprised between 1.7 and 0.7 Myr ago (Morgan et al. 2012, p. 108).

Among the Mode 2 sites, extremely interesting and perfectly preserved remains were brought to light at Isernia La Pineta in Molise (Southern Italy). The chronology

Fig. 10 Olduvai Gorge, site DK (Tanzania): Plan of the *stone circle* and the remains of the occupation surface: Stone artifacts shown in *black*, bones in outline (After Leakey 1971, Fig. 7)

of this site is still rather controversial (Mussi 2001, p. 44), although the new radiometric dates indicate that the locality extends over an area of some 30,000 m^2 and is some 0.60 million years old (Coltorti et al. 2005, p. 19), roughly contemporary with Notarchirico in the same region of central Italy (Orain et al. 2013). It yielded traces of four different occupation layers from which more than 10,000 lithic artifacts, chipped from different raw materials, including limestone and chert from diverse sources, were collected (Peretto 1994a). The site was located along the shores of a lake basin that was later buried by fluvial sediments. The most interesting structural remains were discovered during the beginning of the excavations, when an accumulation of animal bones and stone tools was uncovered on an almost semicircular paleosurface that was very rich in remains of *Bison* skulls and horns and *Rhinoceros* cranial bones and was delimited by large, travertine boulders (Giusberti et al. 1983, p. 100) (Figs. 11, 12 and 13). These discoveries might help interpret the spatial variability and activities carried out within this settlement site (Bartram et al. 1991). Remarkable differences have been noted among the lithic assemblages excavated in different areas of the site, both in the raw material employed for producing artifacts and in the typology and dimension of the stone tools (Fig. 14) (Peretto 1983, p. 81). For example, while flint was mainly used to obtain flakes, limestone was employed for the production of pebble tools, often characterized by the removal of just a few flakes from the distal edge (Peretto 1994b). Traceological studies and the experimental reproduction of the

Fig. 11 La Pineta (Isernia, Southern Italy): A general view of the semicircular animal bones and material culture remains concentration surrounded by limestone boulders, discovered in 1980 (Photograph by P. Biagi)

Fig. 12 La Pineta (Isernia, Southern Italy): *Bison* skull and long bone fragment from the main semicircular concentration discovered in 1980 (Photograph by P. Biagi)

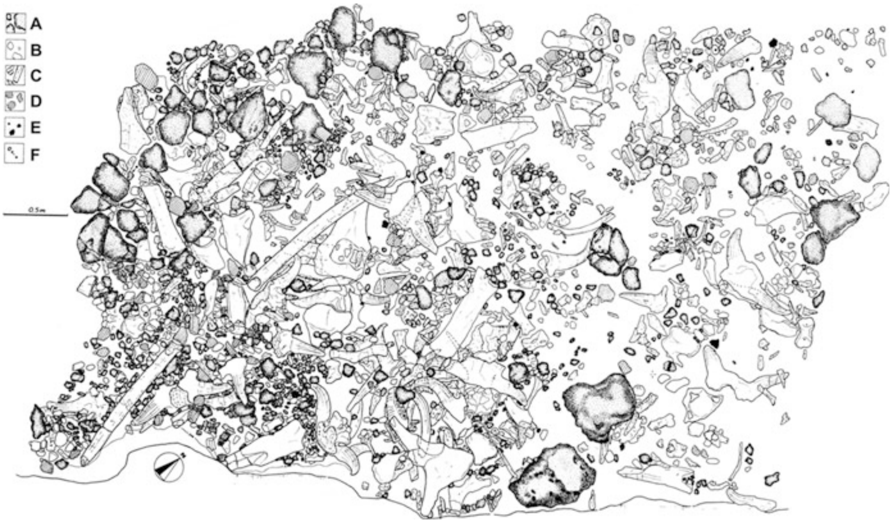

Fig. 13 La Pineta (Isernia, Southern Italy): Plan of the concentration of Fig. 11: (**a**) travertine, (**b**) pebbles, (**c**) faunal remains, (**d**) limestone tools, (**e**) flint tools, (**f**) red lacquerings (After Giusberti et al. 1983)

Fig. 14 La Pineta (Isernia, Southern Italy): Limestone choppers from the surface of the main semicircular concentration (Photograph by P. Biagi)

tool types and their chaine operatoire have shown that small flakes were the most important tools of the Isernia inhabitants, while denticulates that represent some 90 % of the total assemblage are in effect only core waste residuals (Crovetto et al. 1993).

In central Italy, an interesting Mode 2 site dated to slightly later than 0.5 Myr ago, and with an assemblage consisting of both elephant long bones and stone bifacial hand axes, has been excavated at Fontana Ranuccio (Biddittu et al. 1979). The presence of bone hand axes is unique to the area (Biddittu 1982), where they become increasingly more common at the slightly later Mode 2 sites, like Castel di Guido in Latium (Radmilli and Boschian 1996), where the use of elephant carcass bones for making tools has been analyzed in detail (Saccà 2012).

Moving westward, the importance of the remains of structures brought to light by H. de Lumley (1966) at Terra Amata, near Nice, in Provence, is represented by a shallow, oval-shaped hut floor attributed to a Mode 2 group of people who inhabited the region around 0.4 Myr ago. Apart from the exceptional discovery of an almost "intact" habitation structure, the site is important because it yielded the first evident traces of a hearth indicating the use of fire by Paleolithic humans in Europe (de Lumley and de Lumley 2011, p. 41). Traces of fire that have long been suggested from a few Lower Pleistocene sites in East Africa (Clark and Harris 1985; Perlès 1977) are known since some 0.8 Myr ago in Israel (Goren-Inbar et al. 2004), although the reanalysis of 30 Paleolithic sites made a few years before had suggested that controlled fires are not earlier than 0.3 Myr ago, most probably associated with very late *Homo erectus* (James 1996, p. 66) whether this taxonomy is still acceptable according to the new findings (Wagner et al. 2007).

The site of Steinrinne near Bilzingsleben, in central Germany, is of extreme importance for the study of Mode 2 hominids, although the interpretation of its stratigraphy, some 1 m thick, is still debated (Mania and Mania 2005; Müller and Pasda 2011), as well as its chronology, which is referred, according to the different authors, either to 0.42–0.35 Myr ago or 0.25–0.20 Myr ago. The remains of three circular hut foundations, 3–4 m in diameter, with entrances systematically facing southeast and with workshop areas and fireplaces, have been discovered at this camp, dated to some 0.37 Myr ago (Fig. 15). The importance of this site is indicated by the occurrence of the earliest so far known intentionally decorated bone objects that suggest "non-utilitarian behaviours . . . connected to reflexive thinking" (Mania and Mania 2005, p. 110), as well as the indisputable traces of what is claimed to be a ritual paved area "with human skull fragments smashed in macerated condition" (Mania and Mania 2005, p. 113). According to Mania and Mania (2005, p. 114), these discoveries demonstrate that "*Homo erectus* was therefore a human being that had a fully developed mind and culture, capable in creating his own socio-cultural environment with living structures, the use of fire and special activity areas," although other authors prefer to attribute the finds to *Homo heidelbergensis* (Henke and Hardt 2012). This also finds confirmation in the traces of Acheulean "art" both in Africa (Bednarik 2003) and in the Indian subcontinent (Bednarik 1990).

Gran Dolina at Atapuerca in Spain is an even earlier multilayered site, where some kind of ritual activity has been supposed to have taken place. The site yielded 150 human bone fragments, which have been attributed to four individuals,

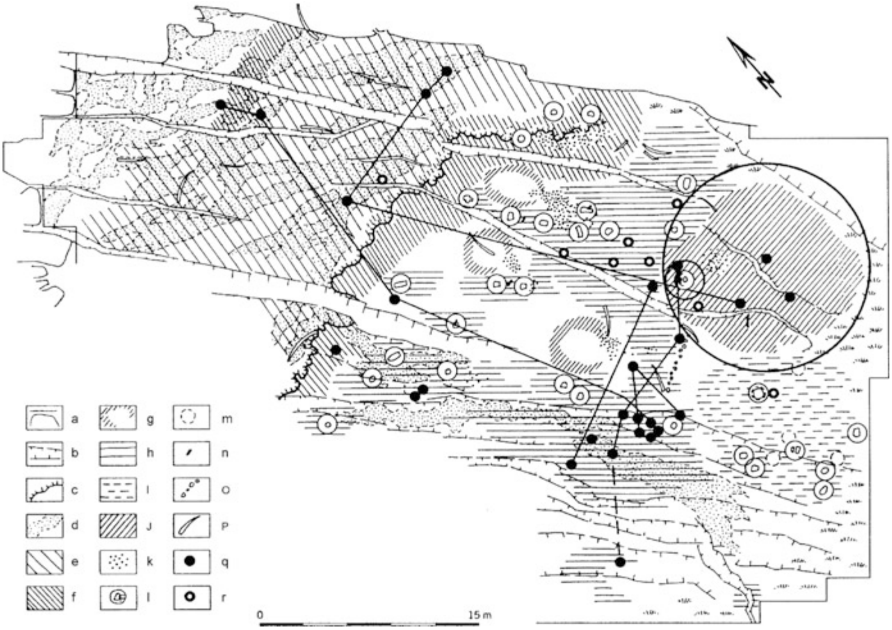

Fig. 15 Bilzingsleben (Germany): Plan of the structuration of the Early Paleolithic camp: (**a**) limits of the excavated area, (**b**) geological fault lines, (**c**) shoreline, (**d**) sandy travertine sediments, (**e**) alluvial fan, (**f**) activity area at the lake shore, (**g**) outlines of living structures, (**h**) workshop areas, (**i**) special workshop area with traces of fire use, (**j**) circular paved area, (**k**) charcoal, (**l**) bone anvils, (**m**) stone with traces of heat, (**n**) bones with intentional markings, (**o**) linear arrangement of stones, (**p**) elephant tusk, (**q**) human skull fragments, (**r**) human tooth (After Mania and Mania 2005, Fig. 7.1)

classified into the new form *Homo antecessor*. Some of the hominid remains from Layer TD6, datable to at least 0.78 Myr ago (Falguères et al. 1999), "show clear cut marks which have been interpreted as evidence of cannibalism" (Mosquera Martínez 1998, p. 17). The chipped stone assemblage from this layer is characterized by relatively small artifacts, among which are utilized flakes, scrapers, denticulates, debitage flakelets, and by-products suggesting the presence of a living floor where different activities had been performed (Carbonell et al. 1999).

Returning to Mediterranean France, this region is very rich in Lower Paleolithic sites, both open air and in caves. Among the latter, the internal deposits of Lazaret Cave (de Lumley 1969), a late Mode 2 Acheulean site attributed to some 0.12 Myr ago, yielded traces of a unique hut structure that has been reconstructed, thanks to the occurrence of stone walls, fireplaces, and "masses of seaweeds possibly used as bedding for site occupants" (Mellars 1995, p. 285). Although this site does not represent the earliest known evidence of cave structural remains in Eurasia, given the traces of much older man-made stonewalls in China (Fang et al. 2004, Fig. 3) and Central Europe (Cyrek 2003, Fig. 6), Lazaret is the only one from which a detailed reconstruction of the events that took place inside the cave in Late Acheulean times has so far been possible (de Lumley and de Lumley 2011, p. 54).

Hunting Weapons

Although, as mentioned earlier, the excavations carried out at Terra Amata in the 1960s had already revealed the presence of one single fireplace, the almost contemporary hunting site of Schöningen, in North Germany, yielded not only the remains of four hearths, one of which is some 1 m in diameter, but even a charred wooden stick, which might “have functioned as a firehook to feed the fire as well as a spit to roast, and also smoke, strips or pieces of meat” (Thieme 2005, p. 127). This site is extremely important because of the occurrence of both the hunting weapons and the other wooden tools brought to light since 1994, which have radically revolutionized our view of the hunting methods and strategies followed by these hominids. The widely accepted view that early *Homo* was unable to conceive and construct throwing weapons is contradicted by the discovery of sophisticated spears, longer than 2 m, which suggest a long tradition in wood shaping and weapon craftsmanship showing that, in contrast to what was previously supposed, this species had already acquired that complex “sequence pattern of behavioural complexes” (Laughlin 1968, p. 305) commonly labeled hunting, which represent “a way of life . . . that . . . has dominated the course of human evolution for hundreds of thousands of years” (Washburn and Lancaster 1968, p. 293). More precisely, “*Homo erectus* in the Middle Pleistocene was fully capable of organising, coordinating and successfully executing the hunting of big game animals in a group using long-distance weapons” (Thieme 2005, p. 127). Although the Schöningen specimens are not the only wooden pointed tools so far recovered from an Early Paleolithic site in Europe (Conard 2007, p. 2008), they undoubtedly represent the best preserved specimens discovered within a horse-hunting camp, a surface of some 3,500 m^2 of which has already been excavated.

Furthermore, it is important to point out that already in the 1980s, Isaac (1984, p. 17) had considered the use of throwing weapons by early hominids when he wrote “if the Lower Pleistocene tool-making hominids were hunting with equipment, they must have been using spears without stone tips (i.e. pointed staves or horns on staves), clubs, and, perhaps most important of all, thrown sticks and stones,” given that “none of the flaked stone artefacts can plausibly be regarded as ‘weapons’” (!). In effect, it has been widely demonstrated that stone hand axes and cleavers (see, for instance, Gilead 1973) are excellent butchering tools, but not hunting weapons, and, in particular, that “the sinuous retouched edge of a hand-axe retains its meat-cutting efficiency longer than a plain flake edge” (Isaac 1984, p. 15).

Conclusion

Apart from the factors mentioned in the introduction, there are many others that make remains of early structures difficult to interpret. Among these are (1) the impossibility of “detailed” radiometric dating of the events that took place at short-term habitation sites, given that hunters periodically moved from site to site following their subsistence strategies (Binford 1978a, 1980), and (2) the difficulty of proving the supposed contemporaneousness of the structural remains within an apparently "homogeneous" area (Binford 1982). This is true even though it is widely assumed that "in inspecting the contents of a single structure, we can be fairly confident that the associated assemblage was all in use at one time, if not made at the same time" (Deetz 1968, p. 283). Besides the two above-mentioned factors, there are three others of major importance regarding (1) the complete excavation of an occupation unit, an enterprise that has been successfully undertaken only on very few occasions (Clark 1968, p. 277), (2) the functional nature of the (seasonal) site itself (Hehmsoth-Le Mouël 1999, p. 81), and (3) the eventual impact of scavengers on the bone remains originated by human activity (Binford et al. 1988).

With the exception of a limited number of cases reported by Clark for East Africa, and a few others which have been described in the preceding chapters, most sites are characterized by more or less dense concentrations of stone artifacts and bones, often closely related to each other (Binford 1989b, p. 459) although differently disposed according to the activities performed (Stevenson 1991, p. 280), reflecting "a complex system of extraction, manufacture, transport, use, resharpening, re-use, renewed transport and eventual discard" (Isaac 1986, Fig. 15.6). Often, these have been subjected to a certain degree of weathering or represent a (complicated) sequence of depositional events that took place over a period of millennia, forming archaeological palimpsests (Hosfield 2005). Isaac (1968, p. 255) classified such concentrations in three main categories according to the vertical and/or horizontal diffusion of the stone tools. The first two of these "represent sporadic, intermittent occupations of great duration," while the third "can probably be interpreted as fairly stable 'home base.'"

Finally, ethnographic analogies are sometimes uncritically accepted by both archaeologists and anthropologists, who often believe "that modern representatives of past stages of cultural development exist" (Freeman 1968, p. 263), sometimes they are simply unaccepted, considered to be unreliable and nonscientific (Hodder 1982, p. 14), even though "any consideration of the implications for archeological interpretation of new ethnographic data . . . requires an examination of the general relationships between ethnographic observations and archeological reasoning" (Binford 1968).

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ Defining *Homo erectus*
- ▶ Defining the Genus *Homo*
- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Historical Overview of Paleoanthropological Research
- ▶ *Homo ergaster* and Its Contemporaries

- ▶ Modeling the Past: Archaeology
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Modern Humans
- ▶ Overview of Paleolithic Archaeology

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Modeling the Past: Archaeology

Miriam N. Haidle

Contents

Abstract

This chapter looks at the potential explanatory power of archaeology as a paleoanthropological discipline. Through the study of artifacts, archaeology provides insight into human behavior. Five facets of archaeological knowledge can be drawn from the material remains of object-related activities (typological, technological, functional, contextual, and cognitive information), from which other behavioral aspects, like subsistence, settlement, social organization, cultural differences, and the cognitive background, can be derived. Archaeological analyzes face significant constraints, but by integrating results from other disciplines, the limits can be broadened. A brief outline of Paleolithic artifact history shows how this part of the behavior of *Homo* developed and how it is

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M.N. Haidle (✉)
Research Center "The Role of Culture in Early Expansions of Humans", of the Heidelberg Academy of Sciences and Humanities, Senckenberg Research Institute, Frankfurt/Main, Germany
e-mail: mhaidle@senckenberg.de; miriam.haidle@uni-tuebingen.de

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accessible by archaeological remains. Following the question "What could they do?" the basis of cultural behavior as a crucial aspect in human evolution is traced in its biological, historical-social, and individual dimensions.

Introduction: Archaeology as a Paleoanthropological Discipline

Archaeology is the anthropological field that studies the material remains of the behavior of former human populations. The most ancient of these populations is the subject of Paleolithic archaeology, which deals with the material remains of early hunter-gatherers, from the first documented stone artifacts of 2.6 Ma to artifacts showing the initial steps toward sedentary life and agriculture at the end of the last Ice Age. Paleolithic archaeology studies artifact assemblages made of stone and organic material by hominins. Additionally, faunal, botanical, and sedimentary remains from early human contexts are examined to gain a broad picture of the hominin behavior and the environment. Paleolithic artifacts and associated finds provide clues to subsistence, social, and cultural behaviors and attest to hominins' increasing capabilities and efforts to get beyond the physical limits of their bodies by using tools. Although tool use and manufacture do occur occasionally in the animal kingdom – ranging from the use of unmodified objects in one specific context that some species of invertebrates, insects, birds, and mammals have developed to the tools adaptive to different problem settings that primates, especially great apes, and some bird species, namely, crows, tend to use – tools emerge within a broadening cultural setting as an eminently human product, as will be described below. For modern humans, who have created a culturally dominated world, tools are second nature. How we got from our occasionally tool-using primate ancestors, with limited cultural capacities and relatively narrow ecological boundaries, to a species that is helpless without tools, but that due to increased cultural capacities is able to perform a huge variety of flexible responses to a wide range of environmental requirements, can be traced only by following the development of artifact assemblages. Therefore, this chapter will focus on the potentials and limitations of interpreting artifacts and tools found in archaeological contexts in illuminating this special human character.

From Primary Field Data to Archaeological Interpretation

The main purpose of archaeology as a discipline is to study artifacts (Fig. 1) made and used by prehistoric populations in order to reconstruct human material culture and activity patterns and thereby to elucidate the development of humans as cultural beings. In a broad sense, archaeology can be defined as the search for human activity zones, the recovery and documentation of these zones, and the analyses of remains (artifacts) and their interpretation. To this end the raw data from archaeological excavations (Fig. 2) undergo analysis, and sometimes additional experimental studies (Thomas 2013) are made on the manufacture and use of

Fig. 1 Middle Paleolithic evidence: a hand axe from St. Même, France (Photo: Hilde Jensen, Eberhard Karls University of Tubingen)

Fig. 2 Re-excavation of excavation material at Vogelherd cave, Southwest Germany (Photo: M. Haidle)

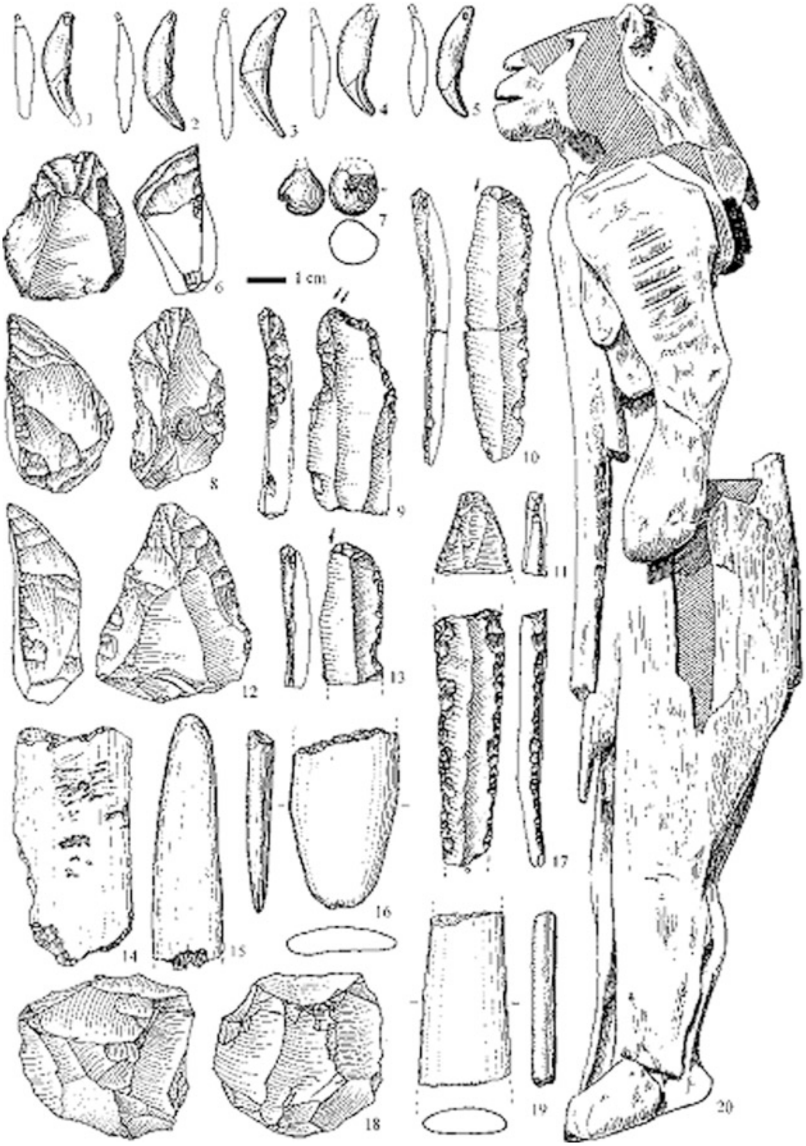

Fig. 3 A selection from the Aurignacian artefact assemblage from Hohlestein-Stadel, Southwest Germany (After Conard and Bolus 2003, p. 344)

artifacts and on the processes through which sites have developed over time. Insights into the origin and formation of artifact assemblages (Fig. 3) may also be gained by examining the object behavior of living human groups via ethnoarchaeology (e.g., Binford 1978; Schiffer 2013) or by comparatively analyzing the material remains of recent and past primate activity (e.g., Mercader et al. 2007).

In sum, artifacts constitute the main material basis of archaeological studies. Additionally, animal bones, plant remains, and sediments from human activity areas are analyzed to provide information on environmental parameters that influenced human behavior (Goldberg and Macphail 2006; VanDerwarker and Peres 2010). Finally, human skeletons can be subject to archaeological research to the extent that they either were directly manipulated – and therefore can be treated as a kind of artifacts – or show physical features induced by certain activities.

What Is an Artifact? What Is a Tool?

"Artifacts" and "tools" are overlapping but not synonymous categories. While tools and their functional use are the main focus of studies of animal behavior, archaeology concentrates on the artificial aspect of manipulating objects in human context. This point of view is summed up by Joachim Hahn (1993), who differentiates among natural objects, items in human context, and things which show signs of human use. Following his definition, the category "artifact" includes all material objects manipulated by humans, from a stone moved by an individual to clearly human-made pits, hearths, and stone structures. More narrowly, Hahn defines artifacts as items of stone, wood, or other materials that show at least some indicative use-wear, whether the objects are separate from or fixed to the environment. The term "tool" bears a technological meaning in archaeology as a subcategory of artifact: They are freely movable objects and were commonly modified in several operational steps, conditions that are not necessary for an object to be accepted as an artifact. Thus, an artifact blank can become a tool intentionally by modification – as in the case of stone flakes reworked into scrapers, denticulates, and burins, for example – or unintentionally by use for some functional purpose, as evidenced by use-wear and retouch on an unmodified blade.

In contrast to the archaeological viewpoint, primatologist Benjamin B. Beck (1980) defines tools not technologically by the object itself, but by the functional use to which an object may be put. Tool use, he writes, is "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool" (Beck 1980, p. 10). Thus, Beck excludes clearly artificial structures like nests, pits, or other fixed artifacts, which are quite commonly constructed by nonhuman animals and are often highly complex, such as the elaborate nests of bower birds, classifying these instead as the material outcomes of different, non-tool behaviors. Ergonomist Christopher Baber (2003, p. 8) identifies a tool as "a physical object that is manipulated by users in such a manner as to both affect change in some aspect of the environment and also to represent an extension of the users themselves. The manipulation is directed towards a specific goal or purpose, and the associated activity requires a degree of control and coordination." Accordingly, in this functional sense, a simple cookie cutter is a tool, but even the most sophisticated cookies themselves are not: They are mere artifacts of tool use (see chapter "▶ Overview of Paleolithic Archaeology," Vol. 3).

The ethological definition of tool use differs from the archaeological one in two ways: Tool use is not restricted to human behavior, and objects fall into the category of tools by their use, irrespective of the technical aspects of use-wear and modification that characterize archaeologically defined tools. Thus, Beck, dealing mainly with directly observed behavior, is only marginally concerned with the material evidence of use on the artifacts, and for zoologists generally, who focus on behavior and often only in passing document the material inventory of populations or species, the technological details are of minor interest. As a result, a major problem in Lower Paleolithic archaeology, namely, identifying artifacts and used objects made from durable material, is excluded from the domain of ethologists studying modern animal tool behavior. For archaeologists, however, who consider the use and manufacture of objects as a characteristic human means to increase the physically limited abilities of the body in solving problems, the functional separation of tool use sensu stricto from the formation of attached or unattached artificial structures is irrelevant. Both can be subsumed under the category of artifacts to get a more complete picture of the material culture, the subject central to archaeology. Which sort of information artifacts yield through archaeological analyses will be discussed next.

Facets of Archaeological Knowledge

Through the use of diverse methodological approaches, five major facets of knowledge can be drawn from archaeological artifacts. These facets can also be combined to generate pictures of different aspects of prehistoric life, like settlement and subsistence behaviors, social and religious organization, technical progress, and the spread of innovations:

- **Typological facet**: Artifacts tell us the forms and styles of objects used by a group. Features of form or style can be categorized by modern analysts into artifact types, yet may not coincide with the originally intended classifications. Changes in types through time, as seen through stratigraphic analysis, seriation, or both, form the basis of relative chronology (see chapter "▶ Chronometric Methods in Paleoanthropology," Vol. 1). The definition of cultural groups and their geographical distribution is founded on the relative chrono-spatial separation of artifact types (Adams and Adams 2008).
- **Technological facet:** Artifacts tell us the materials, devices, and operational steps used to make tools. By analyzing the different operational steps in tool production, their order, and variations in the production sequences known as *chaînes opératoires* (Pélégrin et al. 1988; Schlanger 1994; Bar-Yosef and Van Peer 2009), and also assisted by experiments and ethnoarchaeological studies (McCall 2012), we can gain insight into the basic crafts of past societies. Further, a survey of the implements necessary to make certain artifacts gives evidence on

the complexity of human object behavior. In addition to technological studies, the management of raw material (Andrefsky 1994) is examined to see, for example, if raw material was taken by chance, if certain raw materials were preferred, or if special raw materials were used for particular artifacts. The effort taken to procure the necessary raw materials and the degree of extensive or intensive exploitation are further relevant to developing hypotheses on how former people differentiated and evaluated technological qualities. A combination of typological and technological aspects of knowledge may refine artifact typology and can give information about group- or period-specific employment of crafts.

- **Functional facet:** Artifacts reveal the technological aspects of not only how they were manufactured and got their form but also how they were used. Through experimentation, use-wear and residue analyzes can indicate the activities and ways in which artifacts were employed (Hardy and Moncel 2011; Rots and Williamson 2004; Stevens et al. 2010). Additionally, functional examination can give evidence about behaviors whose resulting artifacts may be only rarely preserved, such as the manipulation of organic raw material (Soffer 2004; Liu et al. 2013). Further, experiments with reconstructions, as in the cases of the wooden spears from Schöningen/Lower Saxony (Rieder 2003) and of Aurignacian bone flutes from the Swabian Jura/Germany (Münzel et al. 2002), can test hypotheses on the qualities of tools. The examination of specific functions related to special artifact types reveals formal categories already set up at the time of the use of the tools. In all, a combination of functional and technological analyses can disclose the life history of artifacts with sequences of repeated modification and use, as well as provide hypotheses as to which functional necessities of a tool influenced its manufacture.
- **Contextual facet**: Artifacts tell us, from their location in a site, where and when they developed, were made and used, and suggest how sites and life within them were organized. Detailed three-dimensional documentation of where objects manipulated by humans, tools, wastes, and associated finds were found (e.g., Speth et al. 2012), combined with refitting of production sequences (e.g., Machado et al. 2013), allows the classification of loci of activity as dump zones, ateliers, food-processing areas, etc. The spatial and chronological relations between the identified activity zones in contemporaneous sites allow conclusions on the broader organization of prehistoric life. The comparison of elements of the environments used or manipulated by humans, in contrast to purely natural assemblages, yields evidence on the specific functional relationships of different hominin groups with the surrounding natural environment.
- **Cognitive facet**: Via the decisions that either deliberately or unconsciously underlay the conceptualization, manufacture, and use of artifacts, we see in them perception, evaluation, memory, planning, knowledge, reasoning, and sociality (e.g., Stout et al. 2008; Wynn and Coolidge 2010). Thus, comparative analysis of data from the four previous facets can reveal preferences in how tools were designed, produced, and used and where on a site they were made or used, pointing up less favored or rejected alternatives. Information on a population's

artifact array, combined with environmental constraints, gives hints about the range of behavioral choice and aspects of decision-making in typology, technology, use of artifacts, and site organization (e.g., Stout et al. 2005). In this way, the spectrum of the decisions taken by a group reveals its knowledge and comprehension of the world, its cognitive capabilities, and the processes of cultural diffusion underlying artifact types, production, and use. In rare cases, as at the French Magdalenian sites of Etiolles (Pigeot 1990) and Pincevent (Ploux 1989) or the Mousterian site Maastricht-Belvédère site K, Netherlands (Stapert 2007), even individual behavior and apprenticeship can be perceived.

In these five aspects of archaeological knowledge derived from artifacts, it becomes obvious that the archaeological discipline is a combination of the sciences and humanities, not only in its questions and collected data but also in its approach to knowledge. While the technical, functional, and contextual aspects are scientifically oriented, yield somewhat reproducible facts, and are open to experimental falsification (not in the hard scientific sense but in the sense that, e.g., wear patterns on a tool can be repeatedly examined and hypotheses on their origin tested), the typological and, even more so, the cognitive facet involve a humanities-oriented hermeneutic approach which nevertheless has to follow epistemological rules (Garofoli and Haidle 2013). This attitude to knowledge looks not so much for identification of facts and rules, but for understanding of background patterns. Of course, this differentiation between scientific-empirical and humanistic-hermeneutic approaches in archaeology can reveal only tendencies: Almost all archaeological works are a mixture of scientific observations and resulting statements with hermeneutic interpretation. The gradual preference of the one or the other depends very much on the theoretical standpoint of the analyst.

Limits to Archaeological Analyses

Despite the discipline's remarkable insights into otherwise undisclosed aspects of everyday life, archaeology is able to give only an incomplete and fragmented picture of prehistoric activities and behavior. Several preconditions have to be met if archaeological analysis is to gain access to at least some sectors of hominin living (e.g., Audouze and Enloe 1997).

First, to become archaeologically evident today, behavior in the past must have caused a detectable change in the natural environment, producing artifacts or leaving other material traces behind. This prerequisite severely limits archaeological studies to a small, but nonetheless important, portion of the full range of human behavior.

Second, the artifacts must have been embedded in sediment, and the sedimentation should have proceeded quickly but not aggressively, so that the activity context of the artifacts is properly sealed. This is a key point, for large parts of the record can be lost by taphonomic processes in slow or incomplete sedimentation and secondary alterations of the find-bearing strata like erosion and bio- or cryoturbation.

Third, the artifacts must have been preserved over time. A wide range of artifacts made from organic material, for example, is likely to have weathered to unrecognizable shapes or to have decomposed altogether. Physical and chemical destruction of different substances depends very much on climatic and soil conditions, with cave sediments in temperate zones being most favorable for many raw materials and the acidic red soils of tropical regions being among the worst areas for conservation.

Fourth, the artifacts must be discovered. Further, they have to be unearthed along with documentation of their context to reveal the maximum information they still bear. The quantity of archaeological evidence in an area or a period is a direct function of the density of research activities and the exposure of relevant geological strata by natural means or through quarrying or construction work.

Lastly, the traces of behavior kept in the artifacts must be accessible to interpretation. This can depend on actual research paradigms, the possibilities and availability of analytic methods, as well as individual or social limitations affecting the analyst.

In Paleolithic archaeology another problem arises from the difficulties in ascribing artifacts to one of several contemporaneous human species represented by fossil remains in the same region. For example, although the first stone artifacts are widely accepted as the products of early *Homo*, whether *H. habilis* or *H. rudolfensis*, there are also australopithecine/paranthropine candidates for authorship. The hand morphology of *Paranthropus*, in principle, would have enabled them to knap stones (Susman 1991) (see chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3), and it is unclear who made the cut marks on bones associated with *Australopithecus garhi* fossils at Bouri/Ethiopia (de Heinzelin et al. 1999). These uncertain attributions hamper the linkage of behavioral data and information derived from physical-biological context and thus obstruct the deciphering of the evolutionary implications of cultural remains.

Extending the Limits: Archaeology as an Integrative Discipline

Beyond the limits of classical artifact analyzes, archaeology develops its full power by applying methods and integrating results from a wide scope of neighboring disciplines. The archaeological prospection of sites, the documentation of finds, and the analyses of artifacts are completed by geophysical methods like remote sensing, supported by geographical information systems, and assisted by microscopy and 3D scanning. Dates and geological, sedimentological, paleofaunal, and paleobotanical data, as well as derived reconstructions of climatological and environmental change (see chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1), add supplementary information on associated to archaeological layers. Genetic models based on ancient DNA and the DNA of modern populations help to create and test archaeological hypotheses, classifications, and interpretations (see chapter "▶ Ancient DNA," Vol. 1). Ethnographical and ethological data give hints on possibilities of interpretation and on associated aspects of behavior not preserved in archaeological assemblages.

Archaeology as a Paleoanthropological Subject

While clues to the behavior of vanished species and populations are limited, functional morphology may give insights into general aspects of living by analyzing dentitions adapted to certain diets, or limbs allowing special ways of locomotion, or other features of the genetically based layout of the body. From the physique, behavioral possibilities can be ascertained. A generalized hand, with opposable thumb and the capability of power and precision grip, is able to do what a hoof or fin cannot. Fossil skeletons of *Homo* and other hominins show bipedal primates developing lower limbs specialized for long-distance walking and freed-up hands perfect for object manipulation. But the question of whether robust australopithecines in fact used their theoretically capable hands (see above) to produce Oldowan artifacts must remain open, as must the actual use made of the enlarging brains (see chapters "▶ The Evolution of the Hominid Brain," Vol. 3 and "▶ Evolution of the Primate Brain," Vol. 2) that accompanied the evolution of the genus *Homo* (see chapters "▶ *Homo ergaster* and Its Contemporaries", "▶ Later Middle Pleistocene *Homo*," and "▶ Defining *Homo erectus*," Vol. 3). Only a few features observed on skeletons can be attributed to concrete activities; in most cases, rather unspecific characteristics, like robustness of the bones, are hard to interpret (Bridges 1995), and these limitations are compounded by the sparseness of the skeletal database and lack of systematic examination of the modern reference.

More productive are correlations between basic physical capabilities, including the cumulative markers of effort, stress, and nutrition that can be deduced from skeletons, and archaeological remains, which yield detailed information about actual behavioral episodes. This explanatory power of artifacts may be demonstrated with regard to the issue of subsistence as the prominent behavioral aspect that can be derived from Paleolithic archaeological remains. For years the question has been discussed of whether some of the human ancestral groups were hunting or actually scavenging (e.g., Blumenschine et al. 1994). While traces from carcass-processing give evidence of the range of the prey according to species and age distribution (Ferraro et al. 2013), as well as show the use of the different body parts, finds like the spears from Schöningen (see chapter "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3) (Thieme 1997) indicate sophisticated hunting activities among *Homo heidelbergensis* (see chapters "▶ Later Middle Pleistocene *Homo*" and "▶ Neanderthals and Their Contemporaries," Vol. 3). Similarly, clues to the composition of the diet can be gathered not only from the faunal and botanical remains from archaeological sites but also from markers detected on artifacts. Thus, digging for termites, well known in chimpanzees (see chapters "▶ Theory of Mind: A Primatological Perspective" and "▶ Great Ape Social Systems," Vol. 2), may also be likely for *Australopithecus robustus*, based on the use-wear analysis on bone tools (Blackwell and d'Errico 2001). Starch grain analyzes of stone tools demonstrate that the selection and processing of barley and wheat was underway in Southwest Asia at least 12,000 years before these grains were domesticated (Piperno et al. 2004), while residues on grinding stones from Shizitan Locality 14, China, indicate the consumption of roots, tubers, and grasses in the last glacial maximum (Liu et al. 2013). A third example is the control of fire, which reaches back at least 1 Ma at Wonderwerk Cave/South Africa, from which burned bone and ashy plant remains show that burning took place in the cave during the early Acheulean occupation (Berna et al. 2012).

Another important issue in Paleolithic archaeology that is accessible through artifact analysis is settlement behavior. Artifacts from a range of settlement sites, from short-term camps with nonspecific structures to long-term dwellings at favorable locations like the Magdalenian sites of Gönnersdorf and Andernach-Martinsberg in the German Rhineland, yield information on the organization of everyday life and on people's mobility, group size, differentiation, and separation of activities (Street et al. 2012).

It is clear from artifact remains that places reserved for special activities developed quite early in human evolution, underscoring that resource management is a key factor in human behavior. There were repeated purposeful visits of early *Homo* to the 1.6-myr-old MNK Chert Factory Site in Olduvai Gorge Bed II, a tool manufacturing site with more than 30,000 documented artifacts made from raw material brought in from about a kilometer away and distributed over an area at least a kilometer from the site (Stiles 1991; Kimura 1997). At the Middle Pleistocene "horse butchery site" Q2 GTP 17 from Boxgrove, *Homo heidelbergensis* brought six to seven flint nodules from the cliff some hundreds of meters away and flaked them into hand axes for the immediate purpose of cutting up the carcass of a horse (Roberts and Parfitt 1999). In analyzing the raw material and artifact transport to and from such sites, the development of larger and more complex settlement systems and territorial organization in human evolution can be brought to light (e.g., Féblot-Augustins 1999).

As a paleoanthropological subject, archaeology can complement the results of other anthropological disciplines in several ways. In analyzing artifacts, archaeology gathers information from short-term behavioral episodes which originate from singular or repeated events and can be fused to a more general picture of the behavioral aspects of chronologically, spatially, or biologically distinctive groups. Furthermore, comparing these results diachronically opens a cultural-historical dimension, thus making the evolutionary perspective on human behavior, and its underlying cognitive development, accessible in its full range. This will be described in more detail below.

What They Did: A Brief Outline of Paleolithic Artifact History

As an overview on historical knowledge derived from artifacts, this section covers the major behavioral developments in the Paleolithic period which can be extracted from archaeological remains; short sketches only, they are organized in roughly chronological order.

Nearly 3.4-million-year-old cut-marked animal bones from Dikika/Ethiopia give the first evidence of possible tool use by hominins; the tools, however, are lacking so far (McPherron et al. 2010). The earliest artifacts to which hominin authorship is assigned are stone tools reported from Gona, Ethiopia (see chapter "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3) (Semaw et al. 2003), dated to 2.6 Ma BP (Ma). They give evidence of spontaneous secondary tool use, the use of one tool to manufacture another to reach an aim (Kitahara-Frisch 1993), which has thus far been observed only in a hominin context. The use of a hammerstone to produce a flake tool to dissect a carcass represents an extension of the problem-solution distance. This allows the development and use of a set of independent cultural units which can be used as behavioral modules, combined in different ways and put in an effective sequence by acting on and modifying each other (Haidle 2012). Contrary to earlier assumptions that the initial phases of the Early Stone Age (Lower Paleolithic: the Oldowan and the succeeding Developed Oldowan A technocomplexes) could be characterized by a core tool technology with distinctive tool types as intentional end products, experiments have shown that the Oldowan core tools vary with the raw material used and that the main target were cutting tools on flakes (Toth 1985) (see chapter "▶ Over view of Paleolithic Archaeology," Vol. 3). However, besides simple technologies with coarse raw material from which few flakes were detached, there are examples of higher-quality raw material processed in longer operational sequences with up to 70 flakes removed, both unidirectionally and multidirectionally, from both natural and prepared platforms (Kimura 1999; Delagnes and Roche 2005). Flakes, few of which show intentional retouch, served mainly as cutting devices, while cores typologically classified in categories, such as choppers and chopping tools, were used as heavy-duty tools. In the first million years of human stone artifact production, raw material transport rarely exceeded some 5–10 km (Goldman-Neuman and Hovers 2009). No early manufacture of bone tools has been proven so far, yet in rare cases the use of bone has been documented (Brain and Shipman 1993). The earliest sites with Lower Paleolithic artifacts are located in East and South Africa; but by around 1.85–1.78 Ma, the first migrants to West Asia (e.g., Dmanisi: Ferring et al. 2011), and presumably to East Asia, were also equipped with similar technology (see chapters "▶ *Homo ergaster* and Its Contemporaries" and "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3). Sparse archaeological evidence complements fossil finds that point to an early occupation of Europe around 1.3 Ma (Arribas and Palmqvist 2002; Arzarello et al. 2007). Throughout the Oldowan period observed site organization is widely unspecific, with a focus on processing carcasses and/or stone tool production (Stiles 1991). Simple settlement structures have been postulated at Olduvai Gorge, Tanzania, and Melka Kunture, Ethiopia, for example; but these claims are largely rejected today due to possible natural explanations.

With the Acheulean, a new technological concept of large tools on mainly large flakes and bifacially knapped into specific forms like hand axes, cleavers, and picks was introduced in addition to the Oldowan technology around 1.76 Ma (e.g., Kokiselei, Kenya: Lepre et al. 2011). In East Africa, a temporal refinement between 1.75 and 1 Ma has been documented, from crude tools to hand axes with an increased number of flake scars (Beyene et al. 2013). The bifacial technology eventually spread from the early Acheulean sites in Africa to later sites in Asia and Europe (Lycett and von Cramon Taubadel 2008). Although the Acheulean bifacial concept dominates the perception of that period, these artifacts are in fact copresent with flake tools, though these are often – possibly falsely – classified as spatially and/or chronologically distinct industries like the Clactonian and Tayacian in Europe or the Developed Oldowan B in Africa (White 2000). Movius (1949) has observed that East and Southeast Asia seem to have been completely excluded from the spread of the bifacial technology concept, but recent finds from China (e.g., Bose valley: Hou et al. 2000) and Korea (Norton et al. 2006) that date to the Middle Pleistocene cast doubt on this hypothesis. Probable evidence of the control of fire as a typical human artifact is increasing, with finds from Wonderwerk Cave at around 1 Ma (Berna et al. 2012) and at Gesher Benot Ya'akov, Israel, at about 0.79 Ma (Goren-Inbar et al. 2004), although some instances of fire use, such as at Zhoukoudian/China from the end of the Lower Paleolithic period, have been questioned (Weiner et al. 1998).

From the very end of the Lower Pleistocene on, human occupation has also been proven not only for Southern Europe, e.g., at Atapuerca TD6, Spain (Carbonell et al. 1995; Parés et al. 2013), but also for its boreal zone as documented by the artifact assemblages from the English sites of Happisburgh 3 and Pakefield (Parfitt et al. 2005, 2010). Although the material remains of *Homo* behavior become more numerous in the subcontinent from 0.5 Ma on, it is not likely that the whole of Europe was populated continuously. The observed artifact spectrum widens in the Middle Pleistocene with wooden spears and other tools, e.g., from Clacton (Oakley et al. 1977), Schöningen (Thieme 1997), possibly Bilzingsleben (Mania and Mania 1998), and Gesher Benot Ya'aqov (Belitzky et al. 1991). A few flaked bone tools have been documented in that period, but no bone or ivory projectile points (Villa and d'Errico 2001). Possible evidence of nonfunctional artifacts such as at Berekhat Ram (d'Errico and Nowell 2000), Hunsgi (Paddayya 1977), and Bilzingsleben (Mania and Mania 1988) is very scarce. Postulated settlement structures at Bilzingsleben (Mania 1983) and the Grotte du Lazaret (de Lumley 1969) are questioned.

In the final phase of the Lower Paleolithic, and continuing into the African Middle Stone Age and the European Middle Paleolithic, flakes were increasingly retouched to improve or create the working edges of tools like scrapers, denticulates, notched pieces, and special forms of knives. The rising focus on flake tools can also be traced in Levallois technology, a new concept of core preparation in stone knapping that first appeared between 0.3 and 0.2 Ma. The idea of characteristically prepared Levallois cores that allow predetermined flake forms did not replace the older concepts, but was used in addition to them. In the European Middle Paleolithic, distances of raw material or tool transport increase up to 100 km or, in some cases, more (Féblot-Augustins 1999). Artifact assemblages of the Upper Middle Pleistocene also reveal increasing complexity and diversification. Microwear patterns at Sai Island, Sudan (Rots and Van Peer 2006), and Biache-Saint-Vaast, France (Rots 2013), and the use of hafting materials evident, e.g., in birch tar residues on stone flakes at Bucine, Italy (Mazza et al. 2006), and Inden-Altdorf, Germany (Pawlik and Thissen 2011), indicate the manufacture of composite tools in both Africa and Europe by at least 300 Ka, or possibly even earlier (Wilkins et al. 2012). By fusing several independent elements with specific attributes, composites with new qualities were formed. Hafting of stone tools, for example, combines the cutting qualities of a stone tool with qualities of the "handle" and different fixing qualities of binding materials and adhesives. The resulting product possesses new qualities that go beyond those of the parts. This technological augmentation is seen as a critical cognitive development (Ambrose 2010).

Stone tool assemblages in both Africa and Europe show increasing regional, chronological, and perhaps functional variation. Also on both continents, in late Middle Paleolithic/MSA context, there appear bone tools such as intensively used awls (d'Errico et al. 2003) and bone points (Henshilwood et al. 2001). From around 0.1 Ma, there is possible evidence of intentional interment of human bodies; whether these qualify as burials and indicate symbolic behavior is still under discussion (e.g., Sandgathe et al. 2012; Balter 2012; Hovers and Belfer-Cohen 2013). First instances of marine shells probably used as personal ornaments have been known for some 100 ka from the Levant, North Africa, and South Africa from contexts of anatomically modern humans (Bar-Yosef Mayer et al. 2009; d'Errico et al. 2009; Vanhaeren et al. 2006, 2013); rare evidence, however, has also been documented for Neanderthal contexts around 50 Ka (Zilhão et al. 2010; Peresani et al. 2013). Geometric engravings on pigment nodules (Henshilwood et al. 2009; Mackay and Welz 2008) or on ostrich egg shell (Texier et al. 2013) are known from southern African Middle Stone Age sites. Finally, evidence of hearth structures, for example, at Kebara (Meignen et al. 2000), marks a more habitual use of fire (Sandgathe et al. 2011). Heat treatment of stone to improve knapping qualities appears in South Africa around 164 Ka (Brown et al. 2009), and around 73 Ka, fire was presumably used for site maintenance by burning layers of plant bedding (Wadley et al. 2011). Evidence of stone-tipped arrows by around 65 Ka is increasing (Lombard 2011), thus providing the earliest example of the use of complementary tool sets with expendable elements like arrows and thread, which function in combination with enhancing/controlling elements like bows (for arrows) and needles (for thread) (Lombard and Haidle 2012) (see chapters "▶ Overview of Paleolithic Archaeology" and "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," Vol. 3).

The Early Upper Paleolithic, starting at around 40,000 years, is characterized by intensified use of bone, antler, and ivory as raw material. In some regions of the world, a burst of personal ornaments and artistic representations is documented, e.g., rock art as in Western Europe (Valladas et al. 2001; González-Sainz et al. 2013) and probably Australia (David et al. 2013), or mobile art (Conard 2003) and musical instruments (Conard et al. 2009) (see chapter "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," Vol. 3) in caves of the Swabian Alb. Although blades had been elements of the artifact inventories since the Lower Paleolithic, a new technological concept of blade production widely introduced in that period allowed an extended exploitation of the stone cores by optimizing the number of rather uniform blanks. In addition, Upper Paleolithic assemblages show increasing diversification in specific tool types for distinct purposes. Settlement of the European Arctic (Pavlov et al. 2004; Slimak et al. 2011) and of Japan (Takashi 2012) took place in this time period; Australia had become inhabited slightly earlier (O'Connell and Allen 2004; Davidson 2013).

From about 30,000 to roughly 20,000 years ago, the first unquestioned evidence of true burials with symbolic meaning, e.g., at Sungir (Pettitt and Bader 2000), Dolní Věstonice (Klíma 1988; Jelinek 1992), and Krems-Wachtberg (Einwögerer et al. 2006) are documented. Tool types became more and more standardized and regionally diversified. The period is known for an important extension of the find spectrum: evidence of fiber processing (Adovasio et al. 1998), systematic gathering of grass seeds (Piperno et al. 2004), production of unfired and fired clay sculptures (Klíma 1991; Einwögerer 2000), and, for the first time, construction of large and complex settlement structures mainly in the mammoth steppe, for example, at Dolní Věstonice and Pavlov (Klíma 1991). While depictions of animal-human hybrids and of elements of the human body, like vulva signs and hand negatives, are known from the Early Upper Paleolithic, the Middle Upper Paleolithic introduced representations of entire human beings that were extremely rare before (Conard 2009; Neugebauer-Maresch 1989) and that now became part of the parietal and mobile art spectrum in the form of frequent Venus figurines, a few male images, and some portraits. In this period, human occupation was extended to Arctic Siberia (Pitulko et al. 2004; Plumet 2006). Since ca. 20 Ka ceramic containers have been used in East Asia (Wu et al. 2012; Craig et al. 2013). After the last glacial maximum, a new category of artifacts, domesticated animals and plants, started to develop in human cultural contexts. Humans accompanied by the first domesticated animal, the dog (Galibert et al. 2011), migrated from Siberia to the Americas (Leonard et al. 2002), crossing the Beringian land bridge.

In conclusion this brief outline, though only superficial, demonstrates a gradual developmental process of progress, diversification, and intensification in archaeological sites from 2.5 Ma until the end of the Pleistocene. It is important to note, however, that all observations of this period are biased by the decreasing chance over time of artifact conservation. Furthermore, summary views of large time periods and spaces may appear clear-cut but, if examined in detail, become blurred.

What Could They Do? Recovering the Basis

Advanced tool behavior, as observed in great apes (see chapters "▶ Great Ape Social Systems," "▶ Theory of Mind: A Primatological Perspective," and "▶ Cooperation, Coalition, Alliances," Vol. 2) and in the artifact record of *Homo*, is founded to only a minor extent on instincts – genetically based processes automatically released by key stimuli – and is instead derived from cognition. Thus, like all cognitively controlled behaviors, it can be stopped arbitrarily, altered by learning, and improved by experience. However, advanced tool behavior is also founded on social transmission of information, so that not every individual has to find answers to perceived problems on his or her own, but can learn from other group members who apply fitting solutions. The social transmission of information opens up a historical-social dimension of behavioral development, the crucial parameter of cultural behavior. Although basics of cultural behavior have been documented in chimpanzees (McGrew 1992; Whiten et al. 1999), orangutans (van Schaik et al. 2003), bonobos (Hohmann and Fruth 2003), and whales and dolphins (Rendell and Whitehead 2001), cultural evolution is a driving factor in human evolution, revealing unknown spaces for variability and flexible adaptation, for progress as well as regress. The variability is expressed on the group level in different cultural performances, the actual sets of attributes of a group with historical-social developmental aspects in activities and manners and their material or notional manifestations.

The Tubingen model for the evolution of cultural capacities (Haidle and Conard 2011) sees the basis of cultural performances as threefold, with biological, historical-social, and individual dimensions (Fig. 4). The **biological dimension** comprises the biological potential and constraints for cultural behavior – in genes, gene expression, anatomy, and physiology. It is expressed, for example, in the structure of the nervous system and the brain, in sensory perception, in motor and articulation skills, in the form of sociality, and in the abilities to communicate. The biological dimension affects the basic course of life history and the physiological-cognitive potential to perceive, create, learn, and remember cultural traits and the ways in which they can be expressed. For example, the genus *Homo* is characterized by generalized hands facilitating material cultural expressions; by the development of a sound production and perception apparatus enabling language, a specific form of very detailed communication; by an increase of the relative brain size (McHenry and Coffing 2000; Lee and Wolpoff 2003); by changes in brain anatomy (see chapters "▶ Evolution of the Primate Brain," Vol. 2 and "▶ The Evolution of the Hominid Brain," Vol. 3) (Bruner 2010); and by shifts in life history (Schwartz 2012) giving more time for learning. Genetic studies suggest increased gene activity in the brain (Enard et al. 2002) and the mutation of single genes like FOXP2, a gene involved in linguistic articulation (Maricic et al. 2013); their specific roles, however, remain unclear. A modern human possesses markedly different biological equipment for cultural behavior than does a chimpanzee or a dolphin; musicality – which will be referred to below – is one of these biological parameters (Peretz 2006). The species-specific characteristic of the biological dimension of behavioral performances enables the finding of species-specific solutions to species-specific problems. Continuity or change in this dimension in general underlies evolutionary mechanisms like gene replication, mutation, and selection, but it may be partly modified through long-term interaction with the environment and, as part of it, material culture (Fisher and Ridley 2013) (see chapter "▶ Genetics and Paleoanthropology," Vol. 1).

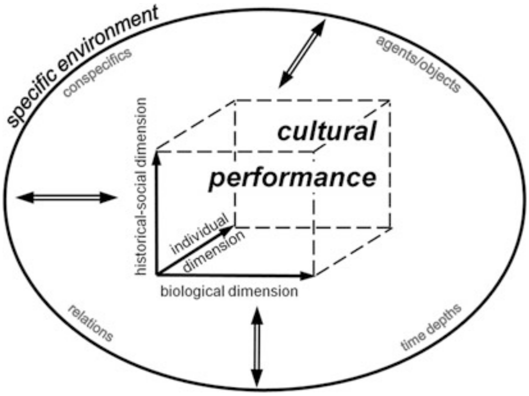

Fig. 4 Tubingen model of cultural evolution showing cultural performance with three dimensions of development (biological, historical-social, and individual). The cultural performance of a group is interdependent with the group-specific environment. This includes conspecifics, agents, and objects as affecting or affected elements with specific relations to the group and in a certain time depth of perception, conception, and action (After Haidle and Conard 2011)

The **historical-social dimension** represents historical and social potentials and constraints. The set of historically acquired knowledge and skills, customs, views, and opinions makes up a part of the individual's environment that can be acted on and used as a basis for further innovation. Social access to the knowledge and skills, customs, views, and opinions can be affected by population density, active communication systems, child-raising habits, teaching systems, systems of religious and political participation, and general group-specific attitudes about learning, innovation, and progress (Rogers 1995). The forms and extent of storage, transmission, permutation, and transformation of the knowledge and skills, customs, views, and opinions support or hamper the unfolding of cultural performances. The historical-social dimension in general affects the ways in which the biological basics are used for cultural behavior, but can also affect the properties of some biological bases (Malafouris 2010; Woollett and Maguire 2011). This dimension unfolds via social transmission from stimulus enhancement to the capacity of teaching, via group-wide adoption of innovations and via transgenerational traditions. The historical-social dimension is self-enhancing; cultural behavior influences factors that foster cultural transmission and creativity (Enquist et al. 2008). An example of the importance of the historical-social dimension is offered by different forms and preferences of musical expression in humans. While there are biological foundations of human musicality and the competence of musical expression and perception (Peretz 2006), historical-social factors determine the different ways in which music is perceived and applied (Cross 2001).

In addition to the biological and historical-social dimensions, cultural performance is defined by a third, **individual dimension**. This dimension reflects individuals' preferences, aversions, skills, and disabilities. The individual dimension incorporates the potential and constraints of an individual, or of a group of individuals, set by the personal social setting and by individual life histories of physical, mental, and emotional experiences. Already in the womb, monozygotic twins with the same genetic complement have different experiences with different epigenetic effects (Petanjek and Kostović 2012). Siblings can be raised in the same family within the same historical-social setting, but nonetheless experience different influences by parents, relatives, friends, teachers, etc., by support or deprivation, by diseases, fortuitous timing, or traumatic accidents. All these factors affect the additional mechanisms of change, which are operative on this dimension: individual learning, personal inventions, and epigenetics, "factors that influence gene expression without modifying the DNA sequence" (Ledón-Rettig et al. 2013, p. 311) (see chapter "▶ Genetics and Paleoanthropology," Vol. 1). Coming back to the music example: while the general musicality of humans is determined by biological factors, the preference for baroque music with cembalo instrumentation, for rock music with electric bass, or for classical Indian sitar music is influenced by historical-social factors, and individual performance in playing one of the instruments depends on individual attraction and training. Wolfgang Amadeus Mozart was a genius with special support by a musician father. He had human, not dolphin, biological capacities and – for his specific work – lived in the favorable historical-social context of eighteenth-century Austria, with orchestras and a broad, fascinated audience, rather than in a small, mobile group as on the Ice Age mammoth steppes.

All of these three major dimensions are multifactorial, and they are not independent. Rather, they influence one another directly or indirectly via reciprocal effects in the context of a specific environment. The latter is the sum of the cultural and social aspects of the environment of an organism or a group, plus the section of the natural environment that affects, or is affected by, the organism or the group. The functional relationships of a group of organisms with elements of the specific environment vary according to the resources they perceive in that environment, given the state of their biological, historical-social, and individual dimensions. Although the natural landscape of a lion and *Homo ergaster* may have been the same, their specific environments differed markedly. These differences include their conspecifics and biotic and abiotic agents, plus objects that they affect or are affected by the form of their relationships with conspecifics/agents/objects and time depth (in perception, conception, and action) in both past and future directions influencing these relationships or behaviors. Cultural performances are thus neither a mere biological product nor solely a historical issue, and they are embedded into the specific environment in which the lives of individuals play out.

While cultural performances represent the actual sets of cultural attributes expressed by an organism or a group, cultural capacities represent the potential range of cultural performances in different subgroups at a given time (Haidle and Conard 2011). The cultural capacity, e.g., of *Homo heidelbergensis* cannot be directly observed, but must be deduced from the sum of quasi-contemporaneous performances seen in the record of material culture preserved at different archaeological sites associated with *H. heidelbergensis* (see chapters "▶ *Homo ergaster* and Its Contemporaries," "▶ Origin of Modern Humans," "▶ Neanderthals and Their Contemporaries," "▶ Later Middle Pleistocene *Homo*," "▶ Defining *Homo erectus*," Vol. 3). The potential cultural capacity of a group, a population, or a species is never completely exhausted by the particular individuals, groups, or populations; rather, different aspects of the capacity are used and expressed.

The range of cultural performances of different groups – and thus the corresponding cultural capacities – has expanded over the course of human evolution. Nonetheless, a single cultural performance in an advanced grade of cultural capacity may be simpler than another performance in an earlier grade (Jones 1995), since different aspects of the full cultural potential can be applied selectively (Hovers and Belfer-Cohen 2006; Lombard and Parsons 2011). The mechanisms of cultural development can be compared with a ratchet (see chapter "▶ Theory of Mind: A Primatological Perspective," Vol. 2) (Tomasello 1999) or better with the act of mountaineering (Lombard 2012); it is always possible to proceed further from any point reached so far, but returning to an earlier or simpler point can also proceed by retracing or following other routes. Using the mountaineering metaphor, cumulative cultural capacity does not only include those cultural efforts that are built upon the highest level achieved but also recursions following on seemingly more advanced solutions. Advanced cultural capacities are not necessarily accompanied by a progressive line of ever more sophisticated and complex solutions built on earlier ones, but allow increasing technological, cognitive, and behavioral flexibility from very simple to highly complex solutions depending on environmental and biological constraints, historical-social paths, and individual decisions. Thus, although the range of cultural performances expands with increasing cultural capacity, cultural evolution is not always linear progressive. The development of cultural capacity is a systemic process involving the coevolution of the three dimensions outlined above and their interactions with the specific environment.

Cognition and culture are the main basis of what prehistoric groups did, and this is partially expressed in the artifacts that have been preserved to our times. Thus, artifacts are a means for detecting the cognitive and cultural background behind their creation. This is not easy. Indications of prehistoric people's cognitive and cultural potential – what they could think and do – have to be separated out from behavior compelled by the restrictions of the specific environment. Archaeology can help to delineate the cognitive space and cultural capacities of prehistoric groups and to trace the development of the biological, historical-social, and individual dimensions. Yet loss of evidence within the archaeological record must also be factored in; it must be kept in mind that absence of evidence cannot be equated with evidence of absence and in not only material but also cognitive and cultural terms (Gott 2002; Speth 2004). What we can detect in the archaeological record is only a group's minimum cognitive potential and cultural performance, as manifested in artifacts. Cognitive faculties and cultural capacities that are apparently unexpressed in material remains because a group did not represent these faculties and capacities, or because an archaeological analyst failed to recognize them, might have been present; yet researchers can only note the lack of such indications.

Conclusions

Through the study of artifacts, archaeology provides insight into tool use as a major part of human behavior. Five facets of archaeological knowledge can be drawn from the material remains of object-bound activities: typological, technological, functional, contextual, and cognitive. From these, other behavioral aspects, such as subsistence, settlement, social organization, and their cognitive backgrounds, can be derived. The only available evidence, though fragmented, on the development of human behavior comes through diachronic comparison of artifact assemblages. So questions of how prehistoric populations used their cognitive potential and cultural capacities, as determined by biological, historical-social, and individual dimensions and limited by environmental constraints, can be approached only through archaeology.

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The Evolution of Speech and Language

Philip Lieberman and Robert C. McCarthy

Contents

P. Lieberman (✉)
Brown University, Providence, RI, USA
e-mail: Philip_Lieberman@brown.edu

R.C. McCarthy
Department of Biological Sciences, Benedictine University, Lisle, IL, USA
e-mail: rmccarthy@ben.edu

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Abstract

Human speech, language, and cognition derive from anatomy and neural mechanisms that have been shaped by the Darwinian process of natural selection acting on variation but that have roots present in other living species. Language did not suddenly arise 50,000–100,000 years ago through a mutation that yielded an innate "faculty of language" nor does the human brain include an organ devoted to language and language alone. Broca's area is not the center of language. Neural circuits linking local activity in different neural structures regulate complex behaviors. Neural circuits that were present in early mammal-like reptiles play a part in regulating laryngeal phonation, conveying both referential information and emotion. Speech plays a central role, enabling transmission of information at a rate that exceeds the auditory fusion frequency. The unique human tongue enhances the robustness of speech, but Neanderthals and other archaic hominins whose neck and skull proportions preclude their having an adult-like human tongue nevertheless could talk. Comparative studies of present-day apes suggest that hominin "protolanguage" lacking syntax never existed. The neural bases of human language are not domain-specific – in other words, they are not devoted to language alone. Mutations on the FOXP2 transcriptional gene shared by humans, Neanderthals, and at least one other archaic species enhanced synaptic plasticity in cortical–basal ganglia circuits that are implicated in motor behavior, cognitive flexibility, language, and associative learning. A selective sweep occurred about 200,000 years ago on a unique human version of this gene. Other transcriptional genes appear to be implicated in enhancing cortical–basal ganglia and other neural circuits.

Introduction

The findings of studies of the communicative capacities of living species, the biological bases of human language including recent advances in neuroscience and genetics, and the archaeological record suggest that human language has a long evolutionary history. Human language makes use of anatomical structures and brain mechanisms that have deep evolutionary roots. The evolutionary framework proposed by Charles Darwin appears to account for human language, which is linked to the biological bases of other aspects of human behavior including cognition and motor control. Aspects of human anatomy and brain mechanisms that were initially adapted to serve other ends were modified to confer human linguistic capacities. Natural selection acted on mutations that were useful in the Darwinian "struggle for existence," entailing the survival of progeny in particular ecosystems. For hominins, this includes their culture. Thus, culture, defined in a broad sense, must be taken into account.

A wide range of independent studies will be taken into account. These include comparative studies of the behavior, morphology, and neuroanatomy of other species. Traditional "experiments in nature" of the behavioral deficits of human subjects arising from trauma, strokes, and neurodegenerative diseases have yielded insights on the neural bases of motor control, language, cognition, and emotional regulation. The findings and implications of these studies will be reviewed. The findings of neuroimaging techniques such as functional magnetic resonance imaging (fMRI)) and diffusion tensor analysis (DTI) have yielded further insights on both the nature and evolution of the brain bases of language and cognition. Recent genetic studies such as ones comparing the DNA of apes, humans, and extinct hominins provide a fresh starting point for understanding how the human brain was shaped. They point to mutations on transcriptional factors and selective sweeps in the last 500 Ka acting on humans, Neanderthals, and other hominin species. A unique human mutation and selective sweep about 250 Ka may have yielded current human cognitive and linguistic capacities. The archaeological record cannot, in itself, serve as an index of cognitive or linguistic ability, but it has yielded valuable insights that will be taken into account.

Although it is probable that earlier forms of hominin language lacked many of the characteristics of present-day languages, many proposals concerning the precise form of language at any period can neither be verified nor refuted owing to the inherent impossibility of observing behavior in prehistory. However, it is possible to rule out some proposals, such as a "protolanguage" that had words but no syntax (Bickerton 1990). The fact that present-day apes raised in a language-using environment can master simple syntax using sign language or manual phonetic systems rules out this possibility. The evolution of the human tongue, which will be discussed here, likewise rules out Neanderthal language being limited to humming (Mithen 2005). Chomsky's (2012) claim that hominins lacked any form of language until 50 Ka is ruled out by the findings of the studies reviewed here. Chomsky's (1972, 2012) dismissal of natural selection having a significant role in biological evolution also is ruled out by this evidence. Selective sweeps on mutilations on transcriptional genes enhanced cortical–basal ganglia circuits implicated in language cognition and motor control (Enard et al. 2002; Reimers-Kipping et al. 2011; Lieberman 2013; Maricic et al 2013).

The Evolutionary Framework

Charles Darwin in 1859 could not have imagined the progress achieved in our understanding of the biological bases of human language and their evolution. Although imperfect – no one can state with certainty how biological brains work – current findings affirm that the agents for the evolution of language are those proposed by Darwin, natural selection, whereby

> . . .any variation, however slight and from whatever cause proceeding, if it be in any degree profitable for an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving. . .. (1859, p. 61)
>
> And the
>
> . . .fact that an organ originally constructed for one purpose. . .may be converted into one for a wholly different purpose. . .. (1859, p. 190)

Only humans possess language, but its evolution does not appear to involve any singular, uniquely human, evolutionary process. Despite what I view as claims to the contrary by Noam Chomsky and his colleagues, the evolution of the specialized anatomy and neural substrates that confer language derives from these Darwinian mechanisms, as is the case for the specialized capabilities of other species, for example, butterflies or anteaters. Moreover, comparative studies and insights from genetics and neurophysiology show that language has roots that can be traced back in time to extinct species, as is the case for other aspects of human behavior. Some aspects of human language can be observed in other living species. It is also becoming apparent that elements of the neural substrate that confer language are involved in other aspects of cognitive and motor behavior. Current research shows that genes that play critical roles in the development of the muscles, lungs, and brains of other species have been modified through the process of natural selection to enhance human cognitive and linguistic capacities.

The seemingly intractable problem in tracing the evolution of human language is the extinction of the hominin species that represent key intermediate stages in the evolution of language. However, the fossil and archaeological records and current knowledge of the biological bases of human language allow us to rule out implausible scenarios and permit reasonable inferences about the evolution of language.

Communication and Cognition

Human language serves as a medium both of thought and communication, and specialized anatomy has evolved to enhance the robustness of human speech, the default modality by which humans communicate using language. Studies of the functional architecture of the brains of primates and other living species show that activity in different parts of the brain linked in *neural circuits* generally is necessary to carry out a "complex" behavior, whether that is picking up an object, comprehending the meaning and emotional content of a sentence, or changing the direction of a thought process (e.g., Alexander et al. 1986; Kotz et al. 2003; Monchi et al. 2001, 2006a; Simard et al. 2011; Wang et al. 2005; Postle 2006; Lieberman 2000, 2002, 2006, 2013). The operations performed by the linked neural structures' circuits do not, in general, appear to be domain-specific. Neural circuits that are active during cognitive tasks – including arithmetic, sorting objects according to shape or color, shifting cognitive sets, etc. – are also involved in linguistic tasks such as keeping words in short-term "working memory" and comprehending the meaning of a sentence. Debates as to whether language evolved to serve communication or cognition are thus inherently irresolvable. Since language plays a role in virtually all aspects of human culture, it also is difficult to identify any single aspect of behavior (e.g., social interaction) that was "the" factor that led to the evolution of human language. Moreover, the specific form of a language appears to both reflect the needs of a culture and to a degree affect the thoughts and manner in which the speakers of a language view the world (Everett 2012). However, it is clear that language is the primary medium by which people communicate, transmitting the information that constitutes a culture from generation to generation and sharing thoughts from individual to individual in every time and place. It is thus improbable that natural selection facilitating communication had no role in the evolution of language (e.g., Chomsky 2012; Fitch 2010).

Comparative Studies

Comparative studies of species other than present-day humans show that they possess some aspects of human language to a lesser degree. Humans and chimpanzees share a common ancestor that lived about six million years ago (The Chimpanzee Sequencing and Analysis Consortium 2005). Thus, although living apes have also evolved since that epoch, studies of the communicative capabilities of apes can yield some inferences on the linguistic abilities of extinct hominin species. Any aspect of language that can be mastered by present-day apes most likely was present in the early stages of hominin evolution. It is apparent that culture plays a role in the acquisition of linguistic capabilities. Chimpanzees, if exposed to a language-using environment early in life, can acquire active vocabularies of about 150 words, communicating their needs and observations to humans and to each other (e.g., Gardner and Gardner 1969; Savage-Rumbaugh et al. 1985). The linguistic environment can even be one in which chimpanzees use a version of American Sign Language (ASL) to communicate with each other. Chimpanzee Loulis in infancy acquired some ASL proficiency when he could only observe and participate in ASL communication with other ASL-using chimpanzees. Biological capacities that may not be apparent in one cultural setting can be observed in other environments. No one, for example, in 1800 could have thought that cars could routinely pass each other at closing speeds that exceed 150 km/h without massive loss of life. Comparative studies of ape communication show that apes can actively use simple syntax and comprehend spoken words and simple spoken sentences. It thus is improbable that any "protolanguage" lacking words ever existed. Other living species can also comprehend spoken words. Some dogs can learn in one trial to reference the meaning of hundreds of spoken words with specific objects (Kaminski et al. 2004). However, no nonhuman species can talk. Apes instead use manual sign language and other manual system to signify words, lending plausibility to the idea that manual gestures played a significant role in the early stages of language evolution (Hewes 1973).

Human Speech

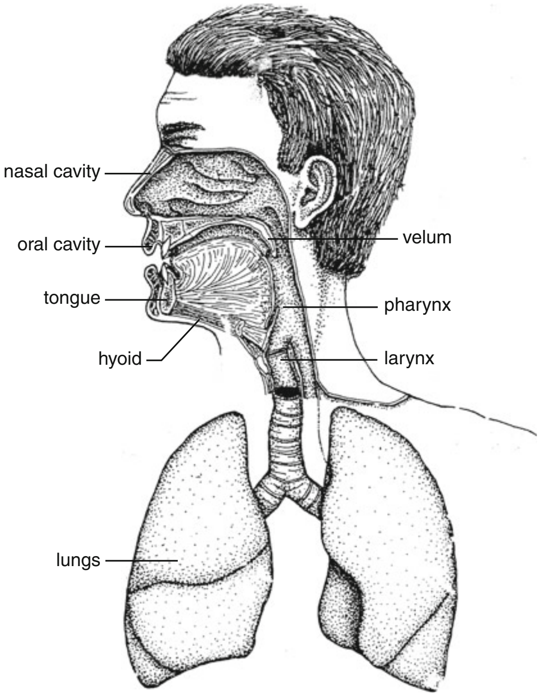
Manual gestures, facial expressions, and body language all continue to play a role in human communication, but speech is the default, primary, phonetic modality of language. Sign languages are a comparatively recent invention, dating to the eighteenth century. Speech confers numerous advantages over communication by means of manual gestures, facial expressions, and posture, such as not having to direct one's attention to individuals who are communicating and freeing one's hands when communicating. However, perhaps more importantly, speech allows humans to rapidly transmit information. The rate at which the sounds that convey words are transmitted exceeds the fusion frequency of the auditory system – the rate at which other sounds merge into a meaningless buzz. The process by which this high transmission rate is achieved has been enhanced through the evolution of the species-specific human tongue and the airway above the larynx. The fossil record thus provides a time line for this process as well as for the evolution of the brain bases for speech motor control, language, and some critical elements of human cognitive ability (Lieberman and McCarthy 2007; Lieberman 2007, 2013). Understanding this process requires some prefatory information on the physiology of speech production.

The invention of pipe organs in mediaeval Europe shows that some knowledge of the physiology of speech production was present. In a pipe organ, a source of acoustic energy with a wide frequency spectrum is filtered by pipes that allow energy to pass through them in narrow ranges of frequency, producing particular musical notes. Johannes Muller systematically described the physiology of speech production in 1848. In Fig. 1 a sketch view of the anatomy involved in speech production is presented.

The lungs provide the source of energy for speech production. Speech is almost always produced during expiration, reflecting the evolutionary history of the lungs. As Darwin pointed out, the lungs of mammals and other terrestrial species evolved from the swim bladders of fish. Swim bladders enabled fish to hover at a particular depth, thereby conserving energy that would otherwise be necessary to move flippers or tails. This is accomplished by storing air extracted from water by gills in elastic sacks, which adjust their body size in order to displace water at a given depth to match their weight. Human lungs retain this elastic property, reflecting the opportunistic, proximate, logic of evolution.

During quiet inspiration, the diaphragm and intercostal and abdominal muscles expand the lungs. The elastic recoil of the lungs then provides the force that expels air during expiration. The duration of inspiration and expiration is almost equal. Since the elastic lungs act in a manner analogous to a rubber balloon, the alveolar air pressure is at a maximum at the start of each expiration and linearly falls as the lungs deflate. The alveolar (lung) air pressure during expiration thus starts at a high level and falls as the volume of the elastic lung sacks falls. The alveolar pressure of the outgoing flow of air impinges on the vocal cords of the larynx. The pattern of activity during speech and singing is quite different. The diaphragm is immobilized. The duration of expiration is keyed to the length of the sentence that a speaker produces, and alveolar air pressure is maintained at an almost uniform level until

Fig. 1 The lungs, larynx, and supralaryngeal vocal tract



the end of expiration. This entails a speaker enabling a set of instructions to the intercostal and abdominal muscles to "hold back" against the force generated by the elastic recoil force, which is high at the start of the expiration and gradually falls. The intercostal and abdominal muscles contain muscle "spindles" that monitor the force that they produce (Bouhuys 1974). The diaphragm contains few spindles, which accounts for its taking no part during speech and singing.

A speaker must anticipate the length of the sentence that he or she intends to produce, generally taking in more air before the start of a long sentence. Since lung volume is higher before the start of a long sentence, the holdback maneuvers of the intercostal and abdominal muscles must take the higher elastic recoil force into account to achieve a relatively level alveolar air pressure during the sentence (Bouhuys 1974).

In his experiments, Johannes Muller found that the rate at which the vocal cords open and close depends on (1) the tension of the muscles that make up the vocal cords, which are complex structures made up of muscles, cartilage, and other tissue, and (2) alveolar air pressure. The fundamental frequency of phonation (Fo) is determined by the rate at which the vocal cords open and close. It is necessary that alveolar air pressure be regulated during speech, as the initial high alveolar air pressure would blow apart the vocal cords, or the fundamental frequency of phonation would start at a very high Fo and rapidly decrease throughout the sentence. This Fo pattern generally does not occur during speech. For most declarative sentences in languages such as English, Fo is more or less level except for momentary controlled peaks that signal emphasis and a sharp decline at the sentence's end (Armstrong and Ward 1926; Lieberman 1967).

Aerostatic and aerodynamic forces and muscle tension acting on the vocal cords of the larynx in all mammals and anurans generate and modulate phonation in much the same manner. However, as Victor Negus (1949) pointed out, the larynges of species that rely on vocal communication, including humans, have been adapted to facilitate phonation at the expense of protecting the lungs from the intrusion of water and reducing the rate at which air can be transferred into the lungs during inspiration. The meaningful calls of many species are differentiated by Fo contours and Fo variations that convey emotional information in all known human cultures and languages. But the fundamental frequency of phonation also conveys linguistic distinctions beyond signaling the end of sentence-like segments and yes–no questions which in English and other languages have rising or level sentence-end Fo contours (Armstrong and Ward 1926; Pike 1945). Local modulation of Fo contours differentiates words in tone languages such as the Chinese languages (Tseng 1981). Many independent studies show that primates signal referential information by means of calls that have different F0 contours (e.g., Cheyney and Seyfarth 1990). This again points out the implausibility of any stage in early hominin communication that relied exclusively on manual gestures.

The Supralaryngeal Vocal Tract and Encoding

The larynx, however, is not the key anatomical structure involved in speech production. Its primary role is that of a *transducer*; the larynx converts the relatively slow flow of air out of the lungs into *phonation.* As the vocal cords open and close an almost periodic series of "puffs" of air enters the airway above the vocal cords, the *supralaryngeal vocal tract* (SVT), that contain acoustic energy at frequencies that are audible. The acoustic energy generated by the larynx is the "source" or energy for phonated vowels such as the vowels and initial consonants of the words *bit* and *map*. Acoustic energy occurs at the fundamental frequency of phonation and at its harmonics, which are integral multiples of Fo.

Movable type is often used as a metaphor to describe the speech signal; speakers ostensibly strung together *phonemes*, segmental sounds approximated by the letters of the alphabet, to form words. The phonemes /t/, /a/, and /b/, for example, can be rearranged to form the words *tab* or *bat*. This, however, is not the case. In the 1960s attempts were made to build devices that would string together phonemes to produce comprehensible speech. The first step appeared to isolate phonemes. It was thought that it would be possible to isolate phonemes, equivalent to the letters of the alphabet, from tape recordings. When a person spoke the word *too*, there hypothetically should be a segment of tape that contained the phoneme /t/ before a segment of tape that contained the phoneme or sound [u] (the phonetic symbol for the actual sound of the vowel of the word *too*). However, much to everyone's surprise, it proved to be impossible to isolate sounds that corresponded to the hypothetical phonemes that formed words. When the segment of recording tape

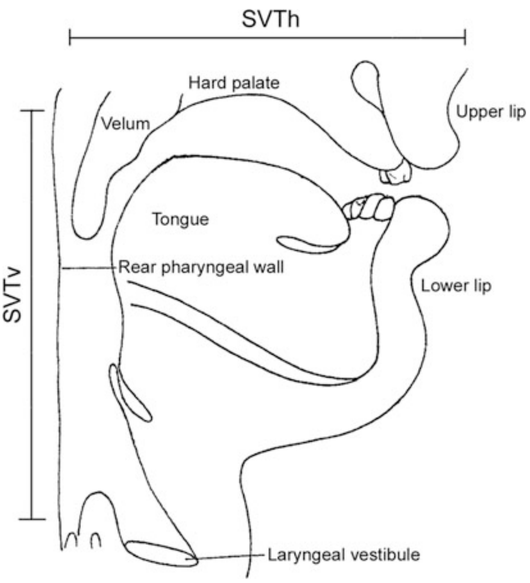


Fig. 2 The adult human tongue and supralaryngeal vocal tract. Half of the tongue, the "SVTh segment," rests in the oral cavity, half the "SVTv segment" rests in the pharynx

that was supposed to correspond to the phoneme /t/ in the word *too* was isolated and linked to the vowel [i] segmented from the word *tea*, the result was incomprehensible. The reason for this phenomenon soon became evident – the position assumed by the lips, tongue, jaw, and larynx for the phoneme /t/ is affected by those necessary to produce the vowel [u] in a different manner than the vowel [i] yielding different overall "encoded" formant frequency patterns for the words *too* and *tea*. It was impossible to segment a "pure" [t] or for that matter any consonant or vowel. Encoding is a general effect. For example, when producing a word such as bit, the position of the tongue, jaw, lips, and larynx which determine the formant frequencies of [b] must move to the different positions necessary to produce [I] (the vowel of this word) and then to produce the [t]. As they move, albeit rapidly, there must be transitions between the SVT shapes of each of the phonemes (see Fig. 2).

Speech allows humans to transmit information at a rate that exceeds that of any other acoustic signal by means of a complex perceptual process. Research at Haskins Laboratories in the 1960s first showed that speech perception involves listeners paying attention to the *encoded*, melded formant frequency pattern that conveys the entire word. The Haskins research program attempted to devise a machine for blind persons that would transform printed texts into speech. They found that it was impossible to find any acoustic signals that would correspond to isolated phonemes. Moreover, when any other nonspeech acoustic signals or mixed tactile/acoustic signals were used to transmit the segmental roughly phonemic representation of words, it was necessary to transmit about 20 phonemes per second to approximate a normal speaking rate. However, the fusion frequency of the human auditory system is about 15 Hz and the hypothetical phonemes would merge into a meaningless buzz. In short, the perceptual unit to which listeners pay attention is the encoded word with the consonant–vowel (CV) syllable being the minimal unit. Listeners perceptually *decode* each word at some internal level, taking account of the constraints of speech production according to the "motor theory of speech perception" (Liberman et al. 1967).

The formant frequency patterns of the hypothetical independent phonemes posited by linguists are always melded together into syllables and words. This seeming deficiency explains why speech is the default medium conveying information through the medium of language. The minimal unit in the speech signal is inherently an encoded CV or longer word sequence. It then can be perceptually decoded into sequences of phoneme. At the neural level, phonemes may be motor-control instruction sets – gestures that a person learns that are instantiated in the motor cortex as *matrisomes*, instructions that guide a set of muscles to perform an act (Sanes et al. 1999). The encoded instruction sets yield the motor acts necessary to produce an entire syllable or word. Segmental un-encoded motor gestures and acoustic cues do not characterize fluent speech. If, for example, a person's lips are viewed when she or he utters the words *too* and *tea* (the syllables [tu] and [ti]), it is apparent that the lips are already pursed and projecting to produce the vowel [u] of *too* at the very start of the syllable. Chinese orthography, which codes words, is a better approximation of the speech signal than alphabetic systems. Successful speech-recognition systems that have been developed since 1967 use algorithms that involve matching the incoming acoustic signal to probable word templates.

The Supralaryngeal Vocal Tract and Normalization

Johannes Muller (1848) realized that the airway above the larynx, *the supralaryngeal vocal tract* (SVT), played a critical role in speech production in a manner similar to a pipe organ. The note that is heard is the product of the organ pipe acoustically filtering the source of sound energy produced by the air flowing through a constriction at the end of the pipe. The airflow through the constriction produces acoustic energy across a wide range of audible frequencies. The organ pipe reduces the amount of sound energy that passes through it at most frequencies. The frequency at which maximum acoustic energy passes through the organ pipe is perceived as the musical note. The length and shape of the organ pipe determines the musical note.

The length and shape of the SVT, which can be thought of as a malleable organ pipe, results in maximum acoustic energy passing through it at *formant frequencies* that are the determinants of individual phonemes along with durational cues. The average formant frequencies of the vowel [i], for example, are 270, 2,300, and 3,000 Hz for the adult males studied by Peterson and Barney (1952), whereas the formant frequencies of the vowel /u/ were 300, 870, and 2,240 Hz. The absolute values of the formant frequencies for any phoneme depend on the length of a speaker's SVT. The average formant frequencies of /i/ and /u/ of the women in Peterson and Barney's study, who had shorter SVTs, were higher. One of the problems encountered in devising automatic speech-recognition systems is how to take into account the effect of speakers' differing SVT lengths. Since the length of the SVT varies from person to person and during the years of childhood and adolescence for the same individual, the absolute values of the formant frequency pattern vary. For example, the formant frequencies of an [i] would be 1.5 times higher for a child whose SVT length was 11.3 cm long than for an adult whose SVT was 17 cm long. Both formant frequency patterns would be perceived as examples of an [i] owing to a speech-specific process of perceptual *normalization* in which listeners internally estimate the length of a speaker's SVT (Nearey 1978). Listeners can estimate SVT length after hearing a short stretch of speech or "reverse engineering" a known phrase such as person saying *hello*. Nearey (1978) showed that the vowel [i] (of the word *see*) was an optimal signal for immediate SVT normalization.

The problem of SVT normalization was evident in one of the earliest studies aimed at achieving speech recognition by machine. Since different speaker's SVTs differ in length, any successful automatic procedure would have to take this into account. Data from Peterson and Barney's (1952) study pointed at [i] (the vowel of see) and to a lesser extent [u] being optimal acoustic cues for SVT normalization. Words having the form [hVd], such as *heed* and *had*, produced by ten different speakers were presented in quasi-random order to a panel of listeners; the listeners had to immediately adjust for different speakers' voices and identify each word. Out of 10,000 trials, listeners misidentified [i] two times, [u] six times, and other vowels hundreds of times. The speakers in Peterson and Barney's (1952) study spoke different dialects of American English, and some had foreign accents, which led to the supposition that dialect differences were responsible for some of the errors. However, Hillenbrand et al. (1995) reported virtually identical results in a study which eliminated dialect variation and made use of computer-implemented technology that was unavailable in 1952 to analyze the speech signals.

The Unique Human Tongue

Charles Darwin raised the question of why the human tongue is so peculiar. Darwin noted:

> The strange fact that every particle of food and drink which we swallow has to pass over the orifice of the trachea, with some risk of falling into the lungs. . .. (1859, p. 191)

In the twentieth century, Victor Negus's studies of comparative anatomy demonstrated both the species-specific nature of the human tongue and the fact that it increased the risk of choking to death on food. Negus concluded that the adult human larynx was carried down into the pharynx because it "is closely apposed to the tongue" (Negus 1949, pp. 25–26). Choking on food remains the fourth leading cause of accidental death in the United States (http://www.nsc.org/library/report_injury_usa.htm). Negus speculated that the unique shape of the human tongue in some manner facilitated speech communication, compensating for increasing the risk of choking. That supposition has been validated by computer-modeling studies that calculate the range of formant frequencies that could be produced by adult human and nonhuman SVTs (Lieberman et al. 1969, 1972; Lieberman and Crelin 1971; Carre et al. 1995; De Boer 2010).

The initial Lieberman et al. (1969) study calculated the formant frequency patterns of the vowels that a rhesus macaque's tongue and SVT could produce. The range of tongue shapes was estimated by taking into account constraints on tongue deformation, which were subsequently confirmed by Takemoto (2001, 2008). The monkey's tongue was positioned as far as possible to produce the SVT configurations used by adult human speakers to yield the "point" vowels [i], [u], and [a]. These vowels delimit the range of vowels used in human languages (Greenberg 1963). The computer-modeling technique showed that the monkey's vowel space did not include these point vowels. Newborn infants have SVTs that are similar to those of nonhuman primates (Negus 1949; Crelin 1969). The SVT computer modeling of Lieberman et al. (1972) used similar techniques to model the SVTs of chimpanzees and human newborn infants.

Crelin had published the first comprehensive anatomy of the human newborn (1969). Crelin concluded that the Neanderthal SVT was similar to that of a large human newborn on the basis of the total pattern of morphological similarities between the basicrania of newborns and the adult male Neanderthal specimen from La Chapelle-aux-Saints. Lieberman and Crelin (1971) produced a computer model of the reconstructed La Chapelle 1 specimen using cineradiographic data on newborn infant cry (Truby et al. 1965) and cineradiographic data on adult human speech (Perkell 1969) to guide the jaw, tongue, lip, and laryngeal maneuvers to derive the range of possible vowels. As Lieberman and Crelin (1971, p. 211) noted, "When we were in doubt as, for example, with respect to the range of variation in the area of the larynx, we used data derived from adult Man that would enhance the phonetic ability of the Neanderthal vocal tract . . ."

At birth in humans, most of the tongue is positioned in the mouth and its shape is flat as is the case for other mammals. The proportion of the tongue in the oral "horizontal" (SVT_H) part of the infant oral cavity relative to the part of the tongue in the "vertical" pharynx (SVT_V) – SVT_H/SVT_V – was 1.5 when the larynx was positioned at its lowest point in the "forceful" cries pictured in Truby et al. (1965, pp. 75–78). The human tongue does not attain its adult 1:1 SVT_H/SVT_V proportions and almost circular posterior midsagittal shape until around 6–8 years of age. The descent and reshaping of the human tongue was determined using cephalometric radiographs of 28 subjects between the ages of 1 month and 14 years. The developmental process by which the species-specific human vocal tract is formed is complex and takes 6–8 years and sometimes as long as 10 years (Lieberman and McCarthy 1999; Lieberman et al. 2001). The length of the oral cavity is first shortened in humans by developmental processes that move the hard palate back on the base of the skull, shortening the nasopharynx (D. Lieberman 2011). The shape and position of the tongue then gradually changes from the newborn tongue, which is flat and is positioned almost entirely in the oral cavity. The human tongue descends down into the pharynx and achieves its posterior rounded contour, carrying the larynx down with it. By 6–8 years of age, SVT_H (the horizontal segment) and SVT_V (the vertical segment) reach the 1:1 proportion. Data from a longitudinal study of 605 subjects imaged using magnetic resonance imaging (MRI) and computed tomography (CT) are consistent with these developmental studies (Vorparian et al. 2009). In contrast, the nonhuman primate tongue is long, rectangular, and positioned primarily in the oral cavity. In fetal development and shortly after birth, the chimpanzee larynx drops slightly owing to an increase in the distance between the larynx and hyoid (Nishimura 2003; Nishimura et al. 2003, 2006, 2008), whereas the human growth pattern involves the descent and shaping of the tongue. Tongue shape and SVT_H/SVT_V proportions in nonhuman primates remain almost constant from birth onward.

The human tongue's oral and pharyngeal proportions and shape explain why only adult humans can produce the vowels [i], [u], and [a] and why these vowels contribute to the robustness of human vocal communication. Half the tongue (SVT_H) is positioned in the oral cavity, and half SVT_V is positioned in the pharynx. SVT_H and SVT_V meet at an approximate right angle, owing to the tongue's posterior circular shape. The extrinsic muscles of the tongue, muscles anchored in bone, can move the almost undeformed tongue to create abrupt midpoint ten-to-one discontinuities in the SVT's cross-sectional area. Stevens's (1972) parallel research explained why the unique human tongue contributed to the robustness of human vocal communication. Stevens showed that only the species-specific human SVT can produce the ten-to-one midpoint area function discontinuities that are necessary to produce the vowels [i], [u], and [a], which he termed "quantal." Stevens employed both computer modeling using Henke's (1966) algorithm and physical models (wooden tubes that could be shifted to change the position of the 10:1 changes in SVT cross-sectional area). Quantal vowels are perceptually salient owing to the convergence of two formant frequencies which yield spectral peaks. Their formant frequency patterns do not shift when tongue position varies about one centimeter about the midpoint. Speakers thus can be sloppy and produce the "same" vowel. Nearey (1978) subsequently showed that the vowel [i] is an optimal signal for determining the length of a speaker's vocal tract – a necessary step in the complex process of recovering the linguistic content from the acoustic signals that convey speech. Whereas the identical formant frequency pattern can represent two different vowels for speakers who have different SVT lengths, no such overlap occurs for tokens of [i].

Independent computer-modeling studies carried out by Lieberman and Crelin (1971), Lieberman et al. (1972); Stevens (1972); Carre et al. (1995), and De Boer (2010) have reached similar conclusions. Carre and his colleagues used a technique that directed the computer model to produce a vocal tract that could produce the full range of formant frequencies of human speech by modifying a nonhuman SVT. The system "grew" a pharynx equal in length to its oral segment. Carre et al. (1995) concluded that in order to produce the full phonetic range of human speech, "a vocal tract must have independently controllable oral and pharyngeal cavities nearly equal in length." The computer-modeling studies of Boë and colleagues (e.g., 2002) have disputed these findings. They claim that Neanderthals and newborn human SVTs have the same phonetic potential as ones having the oral and pharyngeal proportions of human adults. However, their computer model inherently produces irrelevant results because it distorts any SVT into the proportions of a human adult SVT (De Boer and Fitch 2010; Lieberman 2012). A straight plastic mailing tube would also assume the shape and proportions of an adult human tongue during speech using the computer-modeling procedure employed by the Boë studies.

The Linguistic Capacities of Living Nonhuman Species

Syntax and Semantics

The linguistic capacities of other species are seemingly so limited compared to those of humans that they can be ignored. Nonetheless, they can provide insights into the evolution of the different aspects of human language and the role of culture. As noted above, apes raised in environments in which sign language and other manual phonetic means are used can acquire vocabularies of about 150 words. They can also expand the semantic referents of words. The chimpanzee Washoe, for example, used the word *dirty* on her own as an epithet. She had only heard the word before used by the Gardner team to refer to her soiling herself. The limits on the passive vocabulary of chimpanzees have not been determined, but some dogs can learn at least the primary meanings of 200 words (Kaminski et al. 2004). When exposed to a rich human linguistic environment, it is evident that the capacity to learn some aspects of human language exists in other living species. Conversely, humans raised in an extremely deprived linguistic/social environment do not appear to develop either linguistic or cognitive proficiency. Genie, a child locked in a room and virtually deprived of human contact until puberty, failed to develop either normal language or cognitive ability despite intensive therapy (Curtiss 1977). Other less well-documented cases of feral children suggest a similar interaction between the environment and "inherent" biological capacities.

Vocal Tract Normalization and the Range of Speech

The neural basis for vocal tract normalization appears to be genetically transmitted in humans since other species make use of this ability for another purpose – estimating the size of conspecifics and other species from their vocalizations (Fitch 2000).

However, other living species cannot talk. One phonetic limit derives from their tongues. In contrast to the human SVT, the tongues of animals always remain anchored in their mouths during vocalization. Deer, for example, can transiently descend by increasing the distance between the hyoid bone and larynx. The lowered formant frequencies serve to signal to conspecifics that the animal is larger than it actually is. However, the deer cannot change the shape of their SVT to produce quantal speech sounds. This is apparent in the McElligott et al. (2006) study that synchronized audio and video recordings of mature groaning fallow bucks. Their acoustic analyses (e.g., Fig. 1, p. 342) show no change in vowel quality. The deer instead produces the same schwa-like vowel with gradually falling formant frequencies.

Cineradiographs of other mammals vocalizing in Fitch (2000) again show that though transient larynx lowering occurs, the animals cannot produce the shapes necessary to produce quantal vowels because the tongue is still positioned in the animals' mouths. Thus, the dynamic articulatory maneuvers executed by animals discussed in some detail in Fitch (2010, pp. 315–320) do not increase the phonetic range of their vocalizations. Fitch is correct when he notes that the key to the evolution of the human SVT involves the descent of the tongue, not the larynx, which is carried down into the throat as the tongue moves down into the pharynx and is reshaped. However, Fitch overlooks the fact that the SVT shapes that are necessary to produce quantal vowels involve movements of the reshaped human tongue as a whole in the right-angle space formed at the junction of the oral cavity and pharynx. Thus, the undocumented "extinct hominid" discussed by Fitch (2010, p. 318), which has a "flat" nonhuman primate-like tongue anchored in the oral cavity instead of a rounded, human tongue with equal SVT_H and SVT_V segments, could not have produced quantal vowels. Surprisingly, DeBoer and Fitch (2010, p. 41), in their discussion of the vocal tracts of humans and other species, note that the unique attributes of the human tongue and SVT are adaptations for enhancing the robustness of speech communication.

Speech Would Be Possible, Absent the Human Tongue

It is imperative to point out that speech and language are possible without the ability to produce quantal vowels. Lieberman and Crelin concluded in 1971 that the archaeological record demonstrates that Neanderthals must have possessed spoken language in order to transmit their stone-working technology, and in light of the selective advantage of speech's information transfer rate, it is possible to argue that Neanderthals undoubtedly talked. The overall error rate for all vowels in the Peterson and Barney (1952) study was low, only 4.6 %. However, the incremental difference in speech intelligibility that derives from being able to produce quantal vowels is only one example of the fact that small differences drive natural selection. Evolution for adult lactose tolerance, for example, has occurred independently on different genes. It is possible to survive, absent this capacity. The selective advantage was an incremental increase in the food supply (Tishkoff et al. 2007).

As Darwin (1859, p. 61) put it:

> any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relation to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving ... I have called this principle, by which each small variation if useful is preserved by the term of Natural selection.

The Fossil Record of Evolution of the Human Tongue and SVT

Given the advantages of the species-specific vocal tract for speech production, it is of great interest to determine the sizes and shapes of hominin vocal tracts. However, this presents challenges since the hyoid bone is the only component of the SVT that fossilizes, so that indirect approaches are necessary to infer the size and shape of the tongue, larynx, and other soft tissues. Researchers have focused on the bones that directly border the vocal tract – the hyoid, basicranium, mandible, cervical vertebrae, clavicles, and sternum – since these bones constrain the size and shape of the SVT. In addition, researchers have used the comparative method to reconstruct characteristics of the vocal tract in hominins.

Hyoid Bone and Larynx

Eight hyoid bones form the hominin fossil record (see Table 1). Capasso et al. (2008:1007) argued that the lack of muscular impressions on a ~400-ky-old hyoid body from Italy indicates a "reduced capability for elevating this hyoid bone and modulating the length of the vocal tract," whereas Martínez et al. (2008) and Rosas et al. (2006) argued that the archaic hyoid bodies from Sima de los Huesos and El Sidrón, Spain, look nearly identical to those for fully modern humans. Arensburg and colleagues (1989; 1990) argued that the Neanderthal hyoid bone from Kebara, Israel, looks essentially modern, although several of its dimensions fall outside the range of variation of modern humans (Lieberman 1993, 1994; Arensburg 1994). However, it is unclear that there is any relationship between hyoid morphology and SVT length and shape.

The hyoid bone can, however, provide concrete evidence about the presence or absence of air sacs. A hyoid body for a juvenile *Australopithecus afarensis* specimen from Dikika, Ethiopia, exhibits a scalloped dorsal surface identical in morphology to the hyoid bodies of great apes that have laryngeal air sacs (Alemseged et al. 2006). This indicates that loss of air sacs occurred sometime between 3.3 Ma and 600 ky (De Boer 2012). In nonhuman primates, laryngeal air sacs are thought to recycle air from the lungs during long vocalizations (Hewitt et al. 2000) and enhance the impression of the vocalizer's size (De Boer 2009), but their presence limits the ability to produce distinctive speech by reducing the perceptual effects of vowels (De Boer 2009, 2012).

The larynx does not fossilize. However, it is possible to say something about its spatial relationships in hominins using comparative data from nonhuman primates. In humans, great apes, and lar gibbons, the thyroid cartilage is separated from the hyoid bone with the lateral thyrohyoid ligament and triteceum cartilage intervening between the two, which allows the thyroid cartilage to move independently of the hyoid (Bibby and Preston 1981; Nishimura 2003). This is different from the hyolaryngeal configuration in monkeys and agile gibbons, where the hyoid bone and thyroid cartilage overlap. Nishimura et al. (2003, 2006, 2008) showed that the thyroid cartilage descends relative to the hyoid prior to 1 year of age in

Table 1 Hyoid bones in the fossil record

Element	Species	Age (m.y.)	Site	References
Body	*Australopithecus afarensis*	3.3	Dikika, Ethiopia	Alemseged et al. (2006)
Bodies	*Homo heidelbergensis*	0.60[b]	Simo de los Huesos, Spain	Martínez et al. (2008)
Body	*Homo heidelbergensis*[a]	0.40	Castel di Guido, Italy	Capasso et al. (2008)
Bodies	*Homo neanderthalensis*	0.043	El Sidrón, Spain	Rosas et al. (2006)
Hyoid	*Homo neanderthalensis*	0.60	Kebara, Israel	Arensburg et al. (1989)
Hyoid	*Homo sapiens*	0.019	Ohalo II, Israel	Hershkovitz et al. (1995)

[a] Capasso et al. (2008) attributed this hyoid to *Homo erectus*
[b] Date from Bischoff et al. (2007)

chimpanzees, much the same as it does in modern humans. It is therefore likely that descent of the thyroid cartilage relative to the hyoid bone is the first step in a multistage process of laryngeal descent that did not necessarily have anything to do with vocalization (Nishimura et al. 2006). Parsimony would suggest that a thyroid cartilage descended relative to the hyoid and the presence of a lateral thyrohyoid ligament and triteceum cartilage were characteristics exhibited by the last common ancestor of chimpanzees and hominins.

Basicranium

The bones of the palate, vomer, sphenoid, and basioccipital (for the purposes of this paper, the "basicranium") form the roof of the SVT. Several lines of research used the basicranium to reconstruct SVT size and shape in hominin specimens. As noted previously, the first such attempt was by Lieberman and Crelin (1971) and Lieberman et al. (1972), who noted that the "unflexed" basicranium of the adult Neanderthal specimen La Chapelle 1 resembled the basicranium of a human infant or a nonhuman primate. These researchers reconstructed La Chapelle 1 as having a superiorly positioned hyoid and larynx, long SVT_H, and unequal SVT_H: SVT_V ratio. Laitman and Crelin (1976) provided additional justification for this approach, noting that the basioccipital rotates ventrally during early postnatal development, bringing the suprahyoid muscles into a more inferior position and contributing to hyoid and larynx descent. By analogy, fossil hominins with "flexed" basicrania were thought to have low hyoids and larynges in a modern-humanlike configuration, whereas hominins with "unflexed" basicrania were thought to have high hyoids and larynges and an infant human- or nonhuman primate-like tongue and SVT. Laitman and colleagues characterized flexion using a "cranial baseline" spanning the palate, nasopharynx, sphenoid, and basioccipital and reconstructed nonhuman primate-like vocal tracts for paranthropiths, australopiths, and some archaic *Homo* and modern humanlike vocal tracts for OH 12 (*Homo habilis*), Kabwe and Steinheim (archaic *Homo*), Skhūl 5, and late Pleistocene *H. sapiens* (Crelin 1973; Laitman et al. 1978, 1979; Laitman and Heimbuch 1982). The statistical procedure used to characterize the cranial baseline took into account the length of the oral cavity and nasopharynx and the angles formed by the basioccipital, vomer, and palate relative to one another. Other researchers have used on the basicranium to make inferences about SVT size and shape. Budil (1994) used the relationship between flexion and orientation of the styloid process in Petralona (archaic *Homo*) to infer a low hyoid and larynx position for this specimen. Duchin (1990) noted that *H. sapiens*, Neanderthals, and *H. erectus* have similarly shaped oral cavities, suggesting that fibers of three muscles (genioglossus, palatoglossus, mylohyoid) important for movements of the tongue had muscle fiber orientations similar to those of modern humans.

The use of the basicranial angle for reconstructing SVT size and shape has been criticized for a number of reasons. First, it has been noted that many normal human populations have unflexed basicrania, like those exhibited by Neanderthals, but normal vocal tracts (Kean and Houghton 1982; Houghton 1993; Frayer and Nicolay 2000). Carlisle and Siegel (1974, 1978) and Falk (1975) noted that the hyoid in Lieberman and Crelin’s (1971) reconstruction was positioned higher relative to the mandible’s inferior border than is normal in chimpanzees. Lieberman and McCarthy (1999) showed that basicranial flexion and laryngeal descent occur at two entirely different times during ontogeny, suggesting that any effect flexion has on laryngeal descent must be indirect. Although there may be no direct relationship between basicranial flexion, craniofacial shortening, and laryngeal descent, other studies note that the modern human naso- and oropharynx do not leave much room for the hyoid and larynx near the skull base, and space limitations are such that normal increases in size of the adenoids, tonsils, and other lymphatic tissues during childhood often threaten the airway (Tourné 1991).

As noted above, Laitman and colleagues characterized various skulls as either “flexed” or “unflexed” using a cranial baseline. However, these terms do not just refer to flexion of the cranial base in a narrow sense, but to the position of the palate relative to the nasopharynx and basioccipital on the underside of the cranium. The use of terminology most often employed for referring to the orientation of the basioccipital, sphenoid, frontal, and ethmoid bones relative to one another on the inner surface (brain side) of the cranium (see Lieberman and McCarthy 1999) was unfortunate, as it has been a perpetual source of misunderstanding. The statistical procedure employed by Laitman et al. (1979) and Laitman and Heimbuch (1982) clustered together hominin specimens with palates angled relative to the nasopharynx and basioccipital. In retrospect, the real characteristic that determines speech ability is not basicranial flexion, but length of the SVT_H, since this dimension cannot be overly long for there to be a 1:1 proportion. There is not necessarily a link between SVT dimensions and flexion of the basicranium as measured by the cranial baseline. Modern humans are characterized by a large, globular brain and cranial vault; short, retracted palate; short nasopharynx; and flexed basioccipital (Lieberman et al. 2002; Lieberman 2008;

Gunz et al. 2010, 2012). In fully modern humans, these traits are related to a SVT with equal-length horizontal and vertical segments, since the palate, nasopharynx, and basioccipital directly border SVT_H. In chimpanzees and other nonhuman primates, a long palate, long nasopharynx, and unflexed basioccipital form the superior border for a long SVT_H and short SVT_V. However, there is a wider range of variation in these parameters in fossil hominins. Olduvai Hominid (OH) 12, Kabwe, and Steinheim have been reconstructed with "flexed" basicrania, but each of these specimens has a long nasopharynx and long, projecting face. In other words, previous reconstructions based on basicranial flexion and/or palate length (Crelin 1973; Laitman and Crelin 1976; Laitman et al. 1978, 1979; Duchin 1990; Budil 1994) agree with reconstructions based on SVT_H length only insofar as a long nasopharynx and long, projecting face are attributes normally associated with an unflexed basicranium. There is one specimen, Skhūl 5, that has an intriguing combination of features in this regard. This specimen has a relatively long palate but a short, fully modern humanlike nasopharynx and flexed basioccipital. However, in this one case, a moderate SVT_H that does not fall outside the modern human range is incompatible with a 1:1 SVT (see below).

One implication of the above discussion is that one way to rule out certain SVT sizes and shapes is to measure or estimate SVT_H. Since modern humans have a 1:1 SVT, this measurement can then be doubled to estimate hominin SVT length. Using this approach, Lieberman and McCarthy (2007) showed that Neanderthal crania are characterized by a long palate and nasopharynx that forms the roof of a SVT_H that is outside the range of modern humans, and Lieberman and McCarthy (2007) and Granat et al. (2007) reconstructed a SVT_H for Skhūl 5 that falls within the high end of the fully modern human range. SVT_H can be approximated by taking a measurement from prosthion (landmark on the alveolar bone between the central incisors) to the pharyngeal tubercle, which is the point where the pharyngeal constrictors that form the posterior pharyngeal wall attach to the basioccipital, and adding ten centimeters to approximate the anteroposterior length of the lips. Several studies (Boe et al. 2002; Granat et al. 2007) have used basion (landmark on the anterior edge of the foramen magnum) instead of the pharyngeal tubercle to model SVT length. These studies claimed that a modern human-shaped tongue would fit into a Neanderthal head and neck, but did not account for the fact that the posterior pharyngeal wall does not extend all the way back to basion. It is clear that Neanderthals and other archaic hominins have long, projecting faces (Arsuaga et al. 1997; Trinkaus 2003) and that they also would have had long SVT_H dimensions.

Mandible

At one time, it was thought that the genial tubercle, which marks the attachment for the genioglossus and geniohyoid muscles of the tongue to the inner border of the mandibular symphysis, provided the "surest anatomical evidence of speech that the skeleton affords" (Hooton 1946, p. 169; see DuBrul and Reed 1960), although its presence and distribution in modern humans is highly variable. In nonhuman primates, the hyoid body is positioned at the mandible's inferior border at or near the gonial angle. As noted above, Lieberman and Crelin (1971) positioned the hyoid body just superior to the mandible's inferior border in their La Chapelle 1 reconstruction, a move which was criticized at the time. However, it is not the inferior border of the mandible that the hyoid must fall below, but instead the mylohyoid line (which marks the attachment area for the mylohyoid muscle to the deep surface of the mandible) and the attachment sites of the other suprahyoid muscles. The hyoid cannot be positioned much higher than this, since the suprahyoid muscles that attach to the hyoid need to act as elevators, not depressors, of the tongue, in order for the tongue to function in swallowing. There is therefore a constraint on the superior position of the hyoid bone relative to the mandible. Finally, there is some evidence that the resting position of the hyoid may be more superior than previously appreciated in nonhuman primates with normal head and neck postures. The inferior position of the hyoid may be partially an artifact of the manner in which nonhuman primates are positioned for MRI (Nishimura et al. 2008), so that the slightly higher hyoid position reconstructed by Lieberman and Crelin (1971) may fall within a normal range of variation. All hominins, therefore, would have possessed hyoids positioned no higher than the inferior attachment points of the suprahyoid muscles to the mandible's inner border, in close approximation to the mandible's inferior border.

Cervical Vertebrae

In modern humans the hyoid descends below the basicranium, palate, and mandible during ontogeny (Lieberman and McCarthy 1999; Lieberman et al. 2001), but maintains a steady position relative to the cervical vertebrae after 2 years of age. At that age, the superior margin of the hyoid body lies opposite the intervertebral disk between C3 and C4 (Carlsöö and Leijon 1960; Roche and Barkla 1965; Westhorpe 1987). In adults, the hyoid body is positioned as far inferiorly as C4 (King 1952; Bench 1963; Ardran and Kemp 1972), the vocal folds of the larynx lie opposite C5, and the cricoid cartilage lies opposite C6–C7 (Roche and Barkla 1965; Koppel et al. 1968; Wind 1976). It is therefore feasible to infer hyoid and larynx position (and, by extension, SVT_V) by reconstructing neck length in Neanderthals and other hominins that have preserved cervical vertebrae. Table 2 shows the ventral heights of cervical vertebrae C3–C7 for two Neanderthals (La Chapelle 1, La Ferrassie 1) and Skhūl 5. Ventral heights for each of the Neanderthal specimens fall within the low end of the range of modern human data (Arensburg et al. 1990). However, it is clear that, when fit together, Neanderthals would have relatively short necks. McCarthy et al. (n.d.) used an algorithm constructed for humans to estimate intervertebral disk heights and reconstructed neck lengths of about 12 cm for the two Neanderthals and 11 cm for Skhūl 5. For comparison, Trinkaus (1983) estimated Shanidar 2's neck length at 11.5 cm. As noted above, in modern human adults, the vocal folds of the larynx lie opposite C5. Placing the vocal folds of the larynx in the same position produces a ~8 cm long SVT_V for

Table 2 Ventral heights of cervical vertebrae. Data are from Arensburg et al. (1990) and McCown and Keith (1939). Parentheses indicate original authors' estimates based on damaged fossils

Vertebra #	La Chapelle 1	La Ferrassie 1	Skhūl 5	Modern human mean (range)
C3	11.25	12.5	(10.0)	14.1 (11.0–17.0)
C4	(10.6)	12.0	8.5	13.5 (10.3–16.2)
C5	11.5	11.5	9.5	12.7 (10.5–15.2)
C6	12.1	12.5	10.0	12.7 (10.2–15.9)
C7	13.4	13.0	12.5	14.4 (11.2–16.3)

Neanderthals and a 7.5 cm SVT_V for Skhūl 5, which are close to the averages for modern humans. However, SVT_H is so long in these specimens that SVT proportions range between 1.54:1 and 1.60:1.

SVT Reconstructions and Constraints on Hyoid and Larynx Position

A more conservative way to reconstruct SVT shape would be to consider constraints on the position of the hyoid and larynx in the throat. The hyoid bone must be positioned at or below the mandible's inferior border; otherwise, the suprahyoid muscles would not function as elevators of the hyoid during swallowing. Similarly, the hyoid bone cannot lie below the pectoral girdle or else the infrahyoid muscles would not act as depressors of the hyoid, and protraction of the hyoid during swallowing would be impeded by the sternum and clavicles. Taking these constraints into account, the lowest possible position for the hyolaryngeal complex in the three specimens above is for the vocal folds to be at C6, which would put the cricoid cartilage at C7/T1. In this case, La Chapelle 1, La Ferrassie 1, and Skhūl 5 would have SVT ratios between 1.31:1 and 1.33:1, still outside the quantal region (see Fig. 3). The anatomical features that result in unequal SVT ratios are different for the Neanderthal specimens and Skhūl 5. The two Neanderthal specimens have a long palate, long nasopharynx, and short neck, whereas Skhūl 5 has a moderately long palate, short nasopharynx, and short neck.

Schedule of Evolutionary Events

The hyoid, basicranium, mandible, and cervical vertebrae all provide different insights into the evolution of the vocal tract and the timing of the appearance of hominin speech abilities. Comparative data on the spatial relationships between the hyoid and larynx (Nishimura 2003), in combination with ontogenetic data for chimpanzees (Nishimura et al. 2003), indicates that descent of the thyroid cartilage relative to the hyoid body in early infancy arose in an ancestor of extant hominoids, probably for reasons unrelated to vocalization. The origin of a straight bar-like hyoid body sometime between 3.3 My and 600 ky ago indicates the loss of laryngeal air sacs in *Homo erectus* or one of its predecessors or descendants

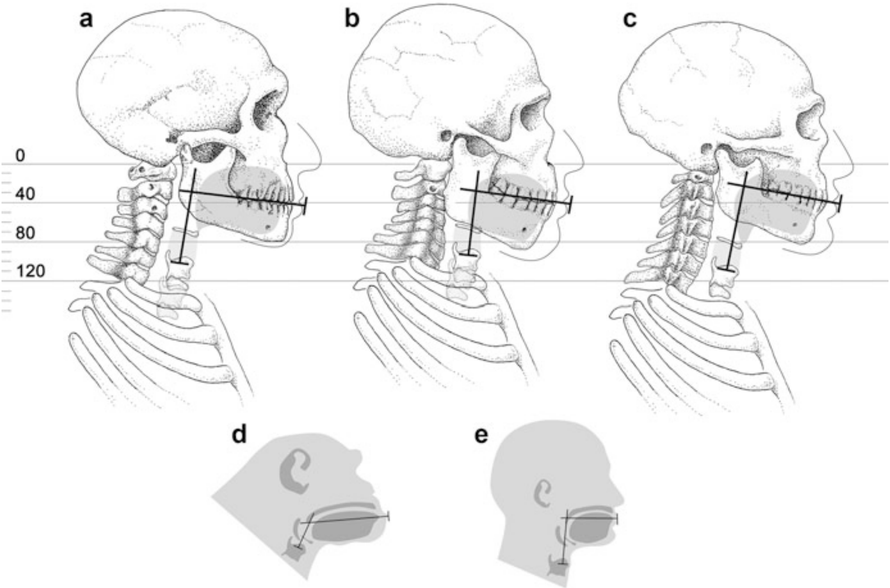


Fig. 3 Position of the hyoid and larynx reconstructed for (**a**) La Ferrassie 1, a Neanderthal, (**b**) Skhūl 5, and (**c**) Predmosti 3, a fully modern human associated with Upper Paleolithic tools. The shaded hyoid and larynx in (**a**) and (**b**) indicate the position of these structures in a hypothetical 1:1 SVT. A (**d**) chimpanzee and (**e**) modern human SVT configuration are provided for comparison

(De Boer 2009, 2012). In great apes, laryngeal air sacs are thought to recycle air from the lungs during prolonged vocalizations. It is known that the nasal cavity, which is parallel to the SVT along the pathway to a speaker's lips, absorbs acoustic energy. This effect degrades the recovery of formant frequencies, reducing speech intelligibility (Bond 1976). Laryngeal air sacs would have had a similar effect, reducing speech intelligibility if hominin speech communication made use of segmental phonemes differentiated in part by their formant frequency patterns. This perhaps accounts for the disappearance of laryngeal air sacs. As noted above, in modern humans, intercostal and abdominal muscles innervated by thoracic nerves are recruited during sustained speech to regulate air pressure. Evidence for an expanded thoracic vertebral canal in Neanderthals and modern humans – and perhaps in *Homo erectus* – may be important in this regard (MacLarnon and Hewitt 2004), although such evidence must remain circumstantial because it is difficult to predict a nerve's cross section from the width of a bony canal, as shown for the hypoglossal canal by DeGusta et al. (1999).

A fully modern humanlike SVT, with equally long horizontal and vertical segments, did not arise until sometime after the appearance of *H. sapiens* 200 ky ago, as the culmination of three distinct processes: (1) shortening of the nasopharynx, (2) shortening of the face, and (perhaps) (3) slight elongation of the neck. Neanderthals and other archaic hominins had a long palate and nasopharynx, a configuration which is associated with a long SVT_H. A long SVT_H cannot be paired with a long SVT_V, unless Neanderthals had necks that were much longer than those of fully modern *H. sapiens*. All available evidence suggests that their necks were short, even if they do fall within the range of variation of modern *H. sapiens*. If one considers the fossil hominins from Mugharet es-Skhūl to be anatomically modern *H. sapiens*, the final two steps in the above schedule occurred after the origin of *H. sapiens*. However, in light of the biological cost of the modern human tongue – an increased propensity for choking to death – it is apparent that speech was the default medium for hominin language before the evolution of a fully modern human tongue. There otherwise would have not been any selective advantage for the retention of mutations and the selective sweep that resulted in the human tongue's proportions. We can thus conclude that the neural substrate for speech production was present in earlier, extinct hominins.

The Neural Substrate for Speech

Neural Circuits

The neural bases of human speech and language have for almost 200 years been linked to discrete localized structures, *organs* of the brain. Locationist theories for the brain bases of language derive from early nineteenth century phrenology. Phrenologists proposed that areas of the neocortex – the outermost layer of the human brain – were the *seats* of complex aspects of human behavior such as piety, language, mathematical ability, and so on (Spurzheim 1815). Each area was devoted to a specific, observable, aspect of behavior. Since direct inspection of the cortex in living subjects was not possible, the area of the skull above the location of the hypothetical seat was the metric that supposedly correlated with the degree to which that behavior was manifested by a particular subject. These claims were tested and were found wanting. When the skulls of clerics were studied, some had exceedingly small areas of their skull at the hypothetical seat for piety. Homicidal individuals instead could be found who had large bumps on their skulls supposedly related to piety and trust.

Phrenology fell into disfavor, but it never died. Paul Broca had decided that the seat of language was not between a person's eyes as Spurzheim had suggested, but Broca operated within the same paradigm. In 1861 Broca published his study of a stroke victim, patient Tan, whose speech was limited to a syllable that sounded like *tan*. Broca limited his postmortem observations to the cortical surface of the patient's brain and linked a cortical area that was damaged to the patient's deficits. Thus, Broca's area was born – a cortical area devoted to language and, according to most accounts, language alone. Broca examined a second patient who had similar speech deficits, in this case also noting damage extending into the basal ganglia, but ignored the subcortical damages. A few neurologists demurred, pointing out the fact that postmortem examinations showed the language and speech were disrupted only when subcortical brain damage was present.

It became evident that Broca's area is not the brain's center of language when the brains of both of the patients examined by Broca were imaged more than a country later. The patients' brains had been preserved in alcohol; a high-resolution MRI of Broca's patient Tan shows that he also had massive damage to the basal ganglia, other subcortical structures, and pathways connecting cortical and subcortical neural structures (Dronkers et al. 2007). Moreover, the left inferior gyrus of the brain – the traditional site of Broca's area in textbook illustrations and published studies – was not the cortical area actually damaged in Tan. Damage occurred anterior to it, close to the ventrolateral prefrontal cortex. After the 1970s, brain imaging techniques such as computerized tomography (CT) and magnetic resonance imaging (MRI) allowed the brains of thousands of patients who suffered aphasia to be examined. Patients who had suffered brain damage limited to cortex that spared subcortical brain structures recovered. Conversely, aphasia only resulted when subcortical structures were damaged. Alexander et al. (1987), for example, documented the speech production deficits of patients who had suffered strokes that damaged the basal ganglia and other subcortical structures, but spared the cortex altogether. The current view, expressed by Stuss and Benson in their comprehensive 1986 study, is that aphasia never occurs without subcortical damage.

Researchers with very divergent positions with linguistic theory share this view in light of the fact that the ventrolateral prefrontal cortex and Broca's area form parts of basal ganglia circuits implicated in regulating speech and language (Lieberman 2000, 2002; Ullman 2004). The brain bases for complex motor acts, such as walking or talking, are neural circuits that link *local* operations performed in different neural structures. While some neural structures, such as those involved in the initial stages of visual perception, are domain-specific, other neural structures perform local operations that constitute elements of different circuits that regulate seemingly unrelated aspects of behavior.

Your car makes use of similar functional architecture. If your car won't start, the repair manual will not instruct you to locate the center of starting. The manual instead will point out a set of linked structures that each performs a local operation. The battery, for example, provides electrical power to the starter motor but it also powers the car's lights, radio, computer, etc., through circuits linking it to these devices. The battery is not in itself the sole device dedicated to electrical power. The generator and voltage regulator form part of the electrical system, and in a hybrid gasoline–electric car, the braking system also charges the battery.

The basal ganglia, subcortical structures that date back in time to anurans similar to present-day frogs, support circuits that link different areas of motor and prefrontal cortex. The basal ganglia operate as a sequencing engine (Marsden and Obeso 1994), regulating motor control and cognition – including aspects of language. Damage to the subcortical basal ganglia or the circuits linking them to cortex explains why the signs and symptoms of aphasia can include speech production deficits, difficulties comprehending the meaning of a sentence, and cognitive deficits. Indeed, although aphasia is usually characterized as a language deficit, Kurt Goldstein (1948), one of the leading aphasia specialists of the twentieth century, pointed out its primary cognitive deficit – loss of the "abstract capacity."

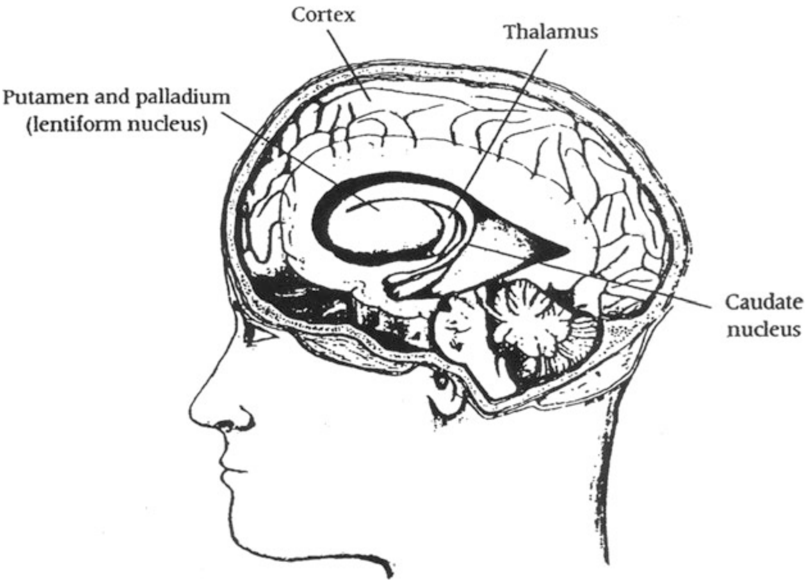


Fig. 4 The basal ganglia and thalamus are positioned deep within the skull. The putamen and globus pallidus (palladium) are contiguous and form the lentiform nucleus

Circuits Linking Cortex and the Basal Ganglia

Invasive tracer studies of the brains of monkeys and other mammals first mapped out a class of circuits that linked areas of motor cortex with the basal ganglia. Retrograde tracer studies entail injecting a chemical or virus that will propagate back down the neural pathway that transmits the electrochemical signals controlling the muscle. The animal must live for a while for the tracer to move down the circuit before being sacrificed. The animal's brain is then sliced into thin sections. Color couplers, similar in principle to those that were used in conventional color film, attach themselves to the tracer and mark out the circuit when the sectioned, color-stained brain tissue is viewed under a microscope. Other tracers can be injected into neural structures that mark the "ascending" neural pathways. Cortical–basal ganglia circuits were discovered that connected areas of prefrontal cortex through the basal ganglia and other subcortical structures to temporal and parietal cortical regions of the brain (e.g., Alexander et al. (1986)). These invasive techniques could not be used to map out human neural circuits, but noninvasive diffusion tensor imaging (DTI) confirmed that these cortical–basal ganglia circuits appear to be similar in humans and nonhuman primates (Lehéricy et al. 2004).

Evidence from studies of neurodegenerative diseases such as Parkinson disease that degrade basal ganglia operations suggested that nonhuman primates and humans had similar cortical–basal ganglia circuits. In Parkinson disease (PD), depletion of the neurotransmitter dopamine degrades the local operations of the basal ganglia (Jellinger 1990). Patients have difficulty in sequencing the submovements that are

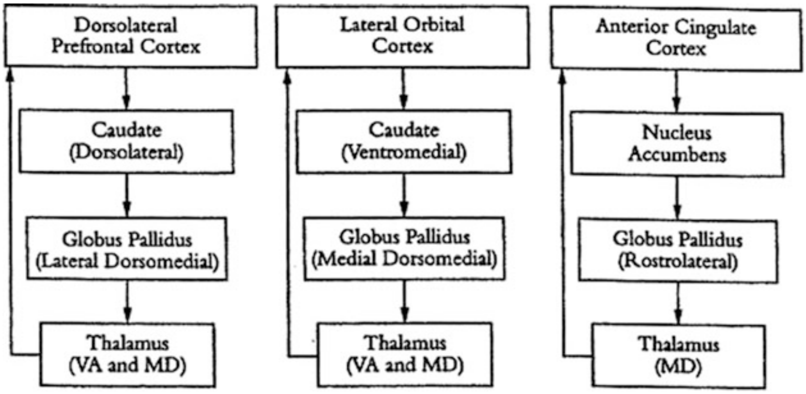


Fig. 5 Studies of the deficits of Parkinson disease and tracer studies of other species formed the basis for three cortical–basal ganglia circuits noted in Cummings (1993). The dorsolateral circuit is involved in cognition, the lateral orbital circuit in emotional regulation, and the anterior cingulate in attention and laryngeal control

necessary to carry out internally directed motor acts such as walking. A common clinical observation is that PD patients who have difficulty walking will do better when they are asked to copy someone walking. An external model allows them to function better. Similar problems occur when PD patients execute manual acts (Harrington and Halland 1991) and speech motor control deteriorates (Lieberman et al. 1992; Lieberman 2006).

Cognitive inflexibility and difficulties performing cognitive acts that require planning or selecting criteria also occur in PD (e.g., Lange et al. 1992). As Alexander et al. (1986), Cummings (1993), and other studies note, prefrontal cortical areas associated with “higher” human cognitive capacities project to the basal ganglia, thus, accounting for cognitive deficits associated with insult to the basal ganglia component of cortical–basal ganglia circuits. A “subcortical dementia” involving profound diminution of cognitive flexibility can occur in Parkinson disease (PD). Patients so afflicted perseverate – in other words, they are unable to change the direction of a thought process or action (Flowers and Robertson 1985; Fig. 5).

Marsden and Obeso (1994) exhaustively reviewed the effects of surgical lesions and dopamine replacement therapy aimed at mitigating the problems associated with PD and concluded that the basal ganglia were a sequencing engine that could link submovements – motor acts stored in motor cortex to carry out an internally guided motor act such as walking. This fit into the traditional view that PD affected motor acts. Marsden and Obeso also noted that when circumstances dictated, the basal ganglia could change a course of action. Focal brain damage limited to the basal ganglia results in similar speech production and cognitive deficits. Bilateral lesions to the caudate nucleus and putamen of the basal ganglia in the subject studied by Pickett et al. (1998) resulted in severe deficits in sequencing the laryngeal, lingual, and lung motor activity necessary to produce articulate speech. The subject had profound difficulty comprehending distinctions in meaning conveyed by syntax that are

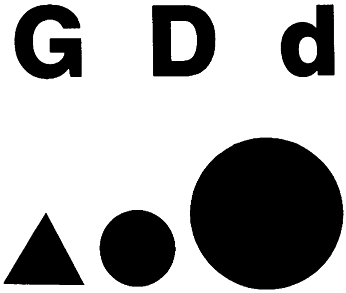


Fig. 6 Two pages of the Odd-Man-Out test. The odd shape or letter of the alphabet can be selected on the basis of either shape or size (uppercase or lowercase for the alphabet). The test subject starts by selecting one sorting criterion but has to shift the criterion after sorting ten cards. This process is repeated four to six times

comprehended by 6-year-old children and was almost incapable of planning her daily activities. When the subject sorted cards in the “Odd-Man-Out” test, which Flowers and Robertson (1985) devised to test PD patients’ cognitive flexibility, she was incapable of changing the sorting criterion. The Odd-Man-Out test uses a pack of cards that each shows three images. For example, the first card might show a large triangle, a small triangle, and a large circle. Subjects are asked to identify the “odd” image on each of ten cards. If the subject had selected shape as the sorting criterion, the circle could be selected. If size was selected as the sorting criterion, the small triangle could be selected. The subjects taking the test are not explicitly given the sorting criteria; they must infer the criteria. The subject can start with either criterion, but after sorting ten cards, the subject is asked to pick a different sorting criterion for the next ten cards and again for at least 14-card sorts. PD patients typically have few errors on the first ten-card sort but have difficulty and high error rates each time that they have to change the sorting criterion. The subject tested by Pickett and her colleagues was unable to even think of a different sorting criterion after successfully completing the first ten-card sort (Fig. 6).

Neuroimaging studies of subjects performing the Wisconsin Card Sorting Test (WCST) confirm the role of the basal ganglia in tasks involving cognitive flexibility and explain why cognitive inflexibility occurs in Parkinson disease. The WCST is an instrument that measures cognitive flexibility – a person’s ability to form cognitive criteria and shift from one criterion to another. The usual form of the WCST entails subjects sorting cards that each have images that differ with respect to shape, color, and number. Subjects have to match test cards to four “reference” cards – a card with one red triangle, a card with two green stars, a card with three yellow + signs, and a card with four green circles. A typical test card might have four yellow stars printed on it. The criterion according to which a test card is matched to one of the reference cards varies and can be the number of images, color, or shape. The subject starts out by making a sort and then is informed whether the sort was “correct” or not. For example, starting with number, matching the test card to the reference card that has four green circles on it would be incorrect if the person running the session wanted to start with color. The subjects then would continue to match by color, receiving a "correct" response until they are being told that the sort was "incorrect" and then having to establish a new sorting criterion without any explicit instruction. After achieving a "correct" response to the new criterion – for example, number – the subject would continue with number, receiving positive feedback until the sorting criterion changed.

The Monchi et al. (2001) fMRI study monitored oxygen levels in the prefrontal cortex, the basal ganglia, and other subcortical structures. Depleted oxygen levels in the ventrolateral prefrontal cortex, the caudate nucleus, and the thalamus confirmed that this cortical–striatal circuit was activated when planning criterion-sorting shifts. Another cortical–striatal circuit that included posterior prefrontal cortex and the putamen was observed during the execution of a sorting criterion set shift. Dorsolateral prefrontal cortex was involved whenever subjects made any decision as they performed card sorts, apparently monitoring whether their responses were consistent with the chosen criterion. Other fMRI studies have replicated these findings and show that the caudate nucleus uses this information when a novel action needs to be planned (Monchi et al. 2006a, 2007).

Similar activation patterns were apparent when subjects were sorting words instead of images and had to match words on the basis of semantic similarity, phonetic similarity of the start of the syllable, or rhyme (Simard et al. 2011). The neural circuits involved thus are not domain-specific, operating solely on visual criteria. Studies ranging from electrophysiological recordings of neuronal activity in the basal ganglia of mice and other animals as they learn tasks (Graybiel 1995; Mirenowicz and Schultz 1996; Jin and Costa 2010) to studies of PD patients (Lang et al. 1992; Monchi et al. 2007) and birds (Brainard and Doupe 2000) also show that the basal ganglia play a critical role in associative learning and in planning and executing motor acts including speech in humans and songs in songbirds. Basal ganglia activity in these cortical–basal ganglia circuits clearly is not domain-specific, i.e., limited to language. Motor activity, associative learning, and cognitive flexibility manifested in both linguistic and visual tasks involve local basal ganglia operations, reflecting the mark of evolution as cortical–basal ganglia circuits were adapted to "new" tasks.

Cortex

Comparative studies of the architecture of the frontal regions of the brains of monkeys and humans have been conducted over the course of more than a century (Brodmann 1908, 1909, 1912). One explanation for why we, but no other primates, can talk and command complex syntax might seem to rest on structural cortical differences. However, this does not seem to be the case. Petrides (2005), in his review of both classical and current studies and his own research, concludes that "the basic architectonic organization" (the distribution of neurons in the frontal layers of the cortex) is the same in humans and monkeys. What characteristics of the human cortical–basal ganglia circuits noted above might allow them to regulate speech motor control and aspects of cognition in humans?

Domain specificity, particularly specificity for language, is inherent in Noam Chomsky's proposal that humans possess a faculty of language devoted to language and language alone. The central premises of Chomsky (2012) and earlier publications and Pinker's (1998) modular view of the brain are that language and other aspects of behavior are each regulated by domain-specific neural circuits and structures. However, noninvasive neuroimaging techniques show that this is not the case. The transmission of information from neuron to neuron in the brain is fueled by burning glucose. Therefore, increased activity in a neural structure uses up more oxygen. Thus, studies using functional magnetic resonance imaging (fMRI), which tracks the level of neural activity in a particular region of the brain by monitoring oxygen depletion, can infer whether a particular cortical area or subcortical structure is active during a task. It is not possible to specify where cortical brain activity is occurring in terms of Brodmann areas on a "standard brain," as is often the practice in neuroimaging studies. Brodmann (1908–1912) microscopically examined brains and found differences in the distribution of neurons in the cortex, which he thought reflected functional differences. The maps that he produced have since been used to refer to delimit areas of the cortex. However, differences in brain morphology make it particularly difficult to identify the particular Brodmann areas in prefrontal cortex (Devlin and Poldark 2007), but some of the local operations performed by different regions of the frontal cortex and in the subcortical components of neural circuits in humans and monkeys are becoming apparent.

The dorsal posterior motor cortex areas control fine motor control during speech and other motor tasks (Petrides 2005). Ventrolateral prefrontal cortex connected to posterior regions by circuits involving the subcortical basal ganglia is active during virtually all tasks that involve selecting and retrieving information according to specific criteria (Duncan and Owen 2000). Dorsolateral prefrontal cortex is active while monitoring motor or cognitive events during a task while taking into account earlier events stored in working memory (Badre and Wagner 2006; Monchi et al. 2001, 2006a, b, 2007; Postle 2006; Wang et al. 2005). These cognitive tasks range from retrieving information and holding it in short-term "working memory" to changing the direction of a thought process.

The Antiquity of Laryngeal Control

The melody of speech which reflects the output of the larynx, or *intonation*, has a deep evolutionary history. Intonation reflects laryngeal activity, and the fundamental frequency of phonation (Fo) and amplitude of speech play a central role in vocal communication, signaling sentence boundaries and other aspects of syntax (c.f., Armstrong and Ward 1926; Lieberman 1967). Controlled Fo contours differentiate words in "tone" languages such as Mandarin Chinese. The neural circuits and anatomy involved in controlling Fo can be traced back to therapsids, mammal-like reptiles who lived during the Triassic, Jurassic, and early Cretaceous lived alongside dinosaurs. The initial role of these structures appears to be mother–infant communication. Studies of human mother–infant communication reveal a special vocal mode or *register*, motherese, by which parents address infants in speech that has a high fundamental frequency of phonation and extreme Fo variation (Fernald et al. 1989). Mammalian infants, (including human infants) also signal for attention by means of a forceful *isolation cry* that has a high Fo and amplitude (Truby et al. 1965) – the cries that can keep parents awake for months. Comparative studies suggest that therapsids employed similar anatomical specializations and neural structures to produce isolation cries. All mammals possess a paleocortex, which includes the anterior cingulate cortex (ACC). The findings of studies of the behavioral effects of damage to the ACC and the neural circuits that connect it to other parts of the human brain show that the anterior cingulate cortex plays a role in controlling Fo and directing attention to virtually anything that one wishes to do. While the soft tissue of the brains of therapsids has not survived, the inference that these mammal-like reptiles had an ACC rests on the fact that they possess three middle ear bones found in all present-day mammals. The initial function of the hinge bones of the reptilian jaw was to open the jaw wide. In the course of evolution, the hinge bones took on a dual role, functioning as "organs" of hearing. This transition from mammal-like reptiles to mammals involved the former jaw bones migrating into the middle ear, where they serve as a mechanical amplifier that enhances auditory acuity. All mammals have both an ACC and these middle ear bones, so that middle ear bones are regarded as an index for the presence of the ACC in mammal-like therapsids.

The Darwinian *struggle for existence* transcends aggressive acts, instead referring to any aspect of behavior that confers a selective advantage and increases reproductive success. Vocal communication that enhances mother–infant contact increases an individual's *biological fitness* and thereby contributes to its reproductive success. Anterior cingular cortex–basal ganglia neural circuits are involved in both attention and laryngeal control and therefore appear to function in that role. For example, lesion studies on mice show that mouse mothers do not pay attention to their infants when neural circuits to the ACC are disrupted (MacLean and Newman 1988; Newman 1985). In adult humans with Parkinson disease, degradation of ACC-to-basal ganglia circuits results in patient apathy (Cummings 1993). *Hypophonation*, an anomalous low-amplitude phonation, is often disrupted in patients with PD (Tsanas et al. 2009), and in extreme cases, PD patients can become mute (Cummings 1993). Virtually every PET or fMRI neuroimaging study ever published shows ACC activity when subjects are asked to perform any task. Our reptilian heritage is evident when an ear ache occurs as result of grinding one's teeth. We retain the "old" nerve pathways between the jaw and bones that have migrated into the middle ear.

An alternate proposal stressing human uniqueness is that laryngeal control in humans derives from a circuit that directly links cortex to the larynx, bypassing the basal ganglia. According to Fitch (2010), this hypothetical circuit is the key to humans being able to learn to talk and the "faculty of language," conferring the ability to form and comprehend sentences that have embedded clauses (Hauser et al. 2002). Fitch also claims that vocal imitation in birds derives from a similar direct cortical-to-laryngeal neural circuit. However, Fitch overlooks evidence that shows that this human-specific hypothetical circuit does not exist.

The basis for Fitch's claim derives from one of the first attempts to study human neural circuits, decades before cortical–basal ganglia circuits were mapped out by tracer studies in other species. Kuypers (1958) attempted to adapt an invasive tracer technique used in early studies on animals to study human brains. The Nauta–Gygax (1954) technique which Kuypers attempted to adapt involves first destroying a discrete part of a living animal's brain. After a few weeks, the animal is sacrificed, its brain is impregnated with a silver solution that highlights neuronal structure, and it is dissected and microscopically examined. The infused silver solution can show damages to *downstream* neurons of the neural circuit that connected them to the structure of the brain that had been destroyed, thereby tracing out a neural circuit. Instead of surgically lesioning any part of a human subject's cortex, Kuypers examined the brains of patients who had died after massive damage to one hemisphere of their brain. Since no one dies because of laryngeal dysfunction (other than from respiratory obstruction), it is difficult to see how this technique could be used to isolate a cortical-to-laryngeal neural circuit. Nonetheless, Iwatsubo et al. (1990) again used the Nauta–Gygax technique to study the brain of an 84-year-old woman who died after two massive strokes. They reported degeneration in spinal cord neurons that they believed revealed a direct cortical-to-laryngeal neural circuit. Jurgens's (2002) review article of 301 studies is cited by Fitch and others to support the claim that this neural circuit is present in humans. However, Jurgens (2002) overlooked damage to basal ganglia and pathways between the cortex and basal ganglia which clearly indicate that the degeneration of brainstem neurons do not constitute evidence for a direct cortical-to-laryngeal circuit. Terao et al. (1997) compared the brainstem neurons of four patients who died from brain damage after strokes with those of four age-matched patients who died from non-neurological diseases. No differences were apparent when the brainstem neurons of the two groups were examined. The neuronal degeneration observed in the Kuypers and Iwatsubo studies therefore may reflect degeneration after death, not downstream damage in circuits linked to cortex.

CT scans and an autopsy of the patient studied by Iwatsubo et al. (1990) showed "massive infarctions of the entire territories of the middle cerebral artery on the right and anterior and middle cerebral arteries on the left." The patient's basal ganglia, pathways to the basal ganglia, and other midbrain and brainstem structures would have been damaged or destroyed by these lesions, resulting in death. Subsequent studies have used noninvasive techniques to study the neural circuits regulating vocalization in living humans. Schulz et al. (2005) used positron emission tomography (PET), which tracks the metabolism of glucose in the brain, to map neural circuits that are active when subjects talked. They concluded that the circuits were a "phylogenetically older system present in all mammals (p. 1845)" involving the basal ganglia and thalamus. As noted above, diffusion tensor imaging (DTI) which directly maps out neural circuits confirms that the human circuits are those present in monkeys and apes (Lehéricy et al. 2004). Fitch apparently overlooked the conclusion of Jurgens's review article. Jurgens (2002, p. 251) concluded that "motor coordination of learned vocal patterns comes from the motor cortex and basal ganglia."

Fitch also takes note of the evolution of vocal imitation in birds to support his claim that direct human cortical control of laryngeal activity is the basis for the evolution of human speech and language. Fitch (2010, p. 352) identifies "X" of the bird brain as the cortical homolog of a circuit similar to the hypothetical Kuypers–Iwatsubo neural circuit. However, area "X" is homologous to the mammalian basal ganglia (Brainard and Doupe 2000).

The Sudden Appearance of Language According to Noam Chomsky

Fitch's hypothetical unique human circuit reflects the position of Noam Chomsky concerning the biological basis of human language. The details of Chomsky's theories have changed over time, but they all posit an innate "faculty of language" that genetically transmits "knowledge of language." In his many publications, Chomsky posits an innate *universal grammar* (UG) that conveys the details of syntax of all human languages. In 1976 Chomsky stated that

> . . .language is as much an organ of the body as the eye or heart or the liver. It's strictly characteristic of the species, has a highly intricate structure, developed more or less independently of experience in very specific ways, and so on. (Chomsky 1976, p. 57)

Chomsky's 2012 model focuses on the proposal made in Hauser et al. (2002) that the faculty of language includes a "narrow" faculty of language, specific to humans, that confers the ability to form and comprehend sentences that contain embedded clause, such as "The boy who fell down was thin." According to linguists following Chomsky's train of thought, sentences having embedded clauses sentence are formed in the human mind by a process of "recursion" that melds simple sentences such as the "The boy is fat" and "The boy fell down" together. It is not clear how Fitch's unique neural circuit to the larynx could account for the evolution of this mental capacity, but that problem is irrelevant because Chomsky's (2012) proposal for the biological bases of human language is outside the framework of evolutionary biology.

Chomsky now claims that human language suddenly appeared between 100,000 and 50,000 years ago by means of a mutation that yielded a mental capacity that he terms *merge*. Following linguistic practice, Chomsky uses the term "rule" *merge* to refer to the mental capacity, the "narrow faculty of language," that yields recursion and complex sentences. Language, in Chomsky's account, was absent before this mutation occurred in one person. The mutation somehow became a characteristic of all human brains, without natural selection playing a role in this process.

Chomsky's theories have been outside of the framework of evolutionary biology for decades. In a 1972 publication, he stated that

> It is perfectly safe to attribute this development [of innate language structures] to 'natural selection', so long as we realize that there is no substance to this assertion, that it amounts to no more than a belief that there is some naturalistic explanation for these phenomena. (Chomsky 1972, p. 97)

The pages of the *Science of Language* (Chomsky 2012) include a sustained argument that natural selection has virtually no role in evolution. Selective sweeps in which a mutation that enhances survival in a particular ecosystem has spread through a human population have been well documented. For example, natural selection acted on different genes to confer the ability to use milk as an additional food source in different parts of the world at different times (Tishkoff et al. 2007). In human settings where domesticated milk-producing animals were absent, adult lactase did not evolve. The interplay between the ecosystem and genetic evolution was stressed by Darwin (1859) throughout *On the Origin of Species*. According to Chomsky and those who share his view, children would not be able to acquire any language because insufficient information supposedly is not present in the utterances that children hear in the early years of life. The syntactic rules, speech sounds, and syllable structures of the language a child hears are acquired because "parameters and principles" that activate them are innate, i.e., genetically transmitted. It's as though all human brains are computers that have identical preloaded software that automatically selects the appropriate instruction set for whatever language a child encounters in the first years of life. In substance, Chomsky's claim is that children do not really learn language in the way that they learn to use forks or chopsticks or the modes of behavior or technology of any human culture. In other words, Chomsky's claim is equivalent to the assertion that no child would "acquire" a language unless this preloaded language software was in his or her brain.

However, natural selection on humans never ended, and this biological certainty demonstrates the implausibility of UG. If anyone's native language was acquired because UG existed, children of Chinese ancestry born and raised in the United States would be unable to fluently speak English. In adult humans, the ability to digest cows' milk is an innate, genetically transmitted biological attribute. In cultures that possessed herds of animals that could be milked, natural selection acted on genetic variations to yield individuals who could digest milk as adults, thereby enhancing their survival and their children's survival. While human cultures exist in which animal husbandry and sources of milk were absent, leading to reduced adult lactose tolerance, language typifies all human cultures.

Virtually all aspects of human life are culturally transmitted, and the primary medium of transmission is language. Thus, if anyone's ancestors had been using any particular language for an extended period – let's say the last 3,000 years (the period when adult lactose tolerance or other attested aspects of human biology evolved) – then if any innate UG were *necessary* to "acquire" that language, natural selection would have acted to enhance survival, optimizing the UG to favor acquiring the particular linguistic characteristics of the indigenous language. The United States is an optimal "experiment in nature" since the ancestors of most Americans did not speak English before their arrival. Since languages differ dramatically, you might have never been able to acquire English if your ancestors were speaking Chinese, Hungarian, or some other language whose structure and sound pattern differs dramatically from English. Natural selection acting over generations would have optimized your innate UG for your ancestral language rendering it deficient for acquiring English. The time depth of the Chinese languages whose syllable structure differs profoundly from that of English would thus prevent Americans of Chinese ancestry from "acquiring" fluent English. Since that is not the case, we can conclude that the innate Chomskian UG does not exist.

Fully Human Linguistic and Cognitive Capability

Brain Size

One aspect of cognitive capability that is apparent in the fossil record is brain size. The first anatomical study of an ape, Tyson's 1699 dissection of an orangutan, revealed many of the anatomical affinities between great apes and humans, but it showed that the ape brain was much smaller than that of any normal adult human. A great deal of attention has since been focused on the human brain being about three times larger than a chimpanzee brain because brains require lots of biological support. Hence, scholars have reasoned that a large brain signifies that it must be useful. Texts on hominin evolution generally include a chart showing an increase in brain size over time. Current assessments show that humans have a scaled-up primate brain with about three times as many neurons (the basic computing elements of all brains) as a chimpanzee brain (Herculano-Houzel 2009).

The size of most parts of the mammalian brain scales up in proportion to overall brain size, but the human brain differs in that the posterior temporal cortex is disproportionately larger than would be expected (Semendeferi et al. 1997, 2002). Temporal cortex is part of the human long-term information storage system. Working memory, the ability to keep information in short-term memory during a cognitive process, appears to access information from permanent memory through neural circuits linking prefrontal cortex to temporal cortex and other structures (Badre and Wagner 2006; Postle 2006). The human prefrontal cortex has long been associated with "higher" cognition and, as noted previously, when linked with the basal ganglia and other neural structures, it is involved in the range of cognitive acts involving "executive control." Dorsolateral and ventrolateral prefrontal cortex work through the basal ganglia as well as through direct neural circuits with information-storing regions of the brain, pulling memory traces of images, words, and probably other stored information into short-term working memory (e.g., Postle 2006; Badre and Wagner 2006; Miller and Wallis 2009).

Although some studies that compared chimpanzee and human brains using magnetic resonance imaging studies have claimed that humans have a disproportionately larger prefrontal cortex, thereby enhancing human cognitive capabilities, that may not be the case. As Semendeferi et al. (2002) noted, MRI scans inherently cannot show that humans have a disproportionately larger prefrontal cortex. The human frontal cortex includes prefrontal as well as posterior areas involved in motor control and, together, these areas are not disproportionately larger than an ape's. It is impossible to differentiate prefrontal cortical areas from the motor regions of the frontal cortex on an MRI. Many proposals have been made for why hominin brains became larger over time. One recurring theory hinges on abrupt climate changes taking place in Africa where early hominins evolved. Alternating periods of frigid glacial cold and heat may have resulted in natural selection for individuals able to think of creative solutions to survival. However, there is no evidence for glacial cold in Africa. Another proposal in the same vein suggests alternating periods of drought and heavy rainfall that resulted in desertlike or lush rain forests in the Rift Valley of Africa as the causal element driving hominin brain size enlargement. However, if archaic hominins responded in a manner similar to other species, the most likely scenario would have involved hominins moving away when the climate became inhospitable. Another theory stressed the ability to communicate with members of one’s group, noting the correlation between group size and size of the neocortex. However, the missing data point is that of solitary orangutans’ brains.

Nonetheless, it is clear that brain size is linked to cognitive ability if only in memory storage capacity. Lartet (1868) noted a gradual increase in brain size in wolves and their prey, and Jerison (1973) and subsequent researchers (e.g., Kondoh 2010) have documented this trend across multiple groups of animals. Acquiring a meal and avoiding being a meal apparently drove the evolution of larger brains. As Darwin (1859, p. 61) pointed out, natural selection will act on any attribute that enhances the survival of progeny in “the infinitely complex relations to other organic beings and to external nature” that all beings face. Given the interlocked neural structures implicated in motor control, cognition, and language, it is improbable that any “one” factor was responsible for driving an increase in hominin brain size.

Transcriptional Genes

Advances in genetics and neurophysiology have unlocked a new means of inquiry into the evolution of human language and cognition. Transcriptional factors are essentially “master” genes that affect the way that other genes are activated to form brains and bodies. Transcription factors are genes that govern the transcription of information stored in DNA into a different form, single-stranded mRNA, which is later translated into functional proteins that make up the building blocks of the body. These proteins bind to DNA sequences near a gene that they regulate so as to control the degree to which they release information to the mRNA. Many members of the extended KE family in London who had severe deficits in speech production, sentence comprehension, and cognitive ability possessed only one copy of the human FOXP2 transcriptional factor, instead of the normal two (Fisher et al. 1998).

The Foxp2 gene is one of many transcription factors that exist in all mammals, birds, and other creatures. The mouse form of Foxp2 (the lowercase spelling indicates that it is not the human version, which is capitalized) controls embryonic development of the lungs, intestinal system, heart, and other muscles as well as the spinal column in mice (Shu et al. 2001). Humans are separated from mice by 75 million years of evolution (Mouse Genome Sequencing Consortium 2002).

The Foxp2 and FOXP2 genes encode a protein that regulates the expression of other genes during processes that mark embryonic development, such as signal transduction, cellular differentiation, and pattern formation. Mutations to other Forkhead transcription factor genes have been implicated in a number of developmental disorders. The areas of expression of FOXP2 and Foxp2 in both the human and mouse brain are similar and include neural structures that form the human cortical–striatal–cortical circuits involved in motor control and cognition – the thalamus, caudate nucleus, putamen, and other subcortical structures (Lai et al. 2003). These neural structures are all intricately interconnected. The cerebellum, which receives input from the inferior olives, is involved in motor coordination. The cortical plate (layer 6), the input level of the cortex, is also affected by the FOXP2 mutation.

The subsequent focus on the role of FOXP2 in human evolution follows from its being one of the few genes that has been shown to differ from its chimpanzee version (The Chimpanzee Sequencing and Analysis Consortium 2005). A "human" version evolved that differs from the version found in chimpanzees during the six- or seven-million-year period that separates humans and chimpanzees. In that period FOXP2$^{\text{human}}$ underwent two substitutions in its DNA sequences, causing two amino acid changes in the FOXP2 protein compared to one amino acid substitution between chimpanzees and mice over the previous 70 million years. The form of FOXP2 that has two amino acid substitutions also occurs in Neanderthals and Denisovans – a group related to Neanderthals. A third change unique to humans occurred in intron 8 of the FOXP2 gene and resulted in a selective sweep during the period in which anatomically modern humans appeared some 260,000 years ago (Maricic et al. 2013).

The date of this "selective sweep" for the unique human form of FOXP2, approximately 260 ky ago, was first established by Enard and colleagues (2002). Selective sweeps occur when a gene confers a significant advantage in the Darwinian "struggle for existence" – an individual's having more surviving children, such as adult lactose tolerance. In most instances it is unclear what the function of a gene is that differs between chimpanzees and humans. However, in this instance, the effects of a FOXP2 anomaly in the KE family showed that it is playing a key role in the attributes of speech, language, and cognition that distinguish humans from chimpanzees and other living species. Members of this extended family who had the anomalous version of FOXP2 had difficulty executing simple orofacial maneuvers – such as simultaneously protruding their tongue while pursing their lips, repeating spoken words, and talking. In addition, these subjects had difficulty comprehending distinction conveyed by syntax, forming sentences, and had as a group, lower scores on intelligence tests (Vargha-Khadem et al. 1995, 1998; Watkins et al. 2002). Anomalies in basal ganglia also were noted (Watkins et al. 2002).

Mouse "knock-in" studies have demonstrated that the human version of FOXP2 enhances information transfer and associative learning in the basal ganglia. In light of basal ganglia activity in both associative learning and motor control, this would account for cognitive deficits in afflicted members of the KE family as well as their inability to learn and execute the complex motor acts that enable us to talk and which also control internally guided motor acts. The human form of FOXP2 was knocked into mice (Enard et al. 2009; Lieberman 2009; Reimers-Kipping et al. 2011). When the human version of FOXP2 was knocked into mouse pups, their vocal calls were somewhat different than the calls of mouse pups that had the normal "wild" version of Foxp2. When the wild form of Foxp2 was knocked out in mouse pups, they died soon after, reflecting its role in lung and cardiovascular development. The critical finding was that the knocked-in human form of FOXP2 conferred increased synaptic plasticity in basal ganglia neurons as well as increased lengths of dendrites in the basal ganglia, thalamus, and layer VI of the cortex. In particular, the human version of FOXP2 increased synaptic plasticity in medium spiny neurons in the basal ganglia and in the substantia nigra, another structure of cortical–basal circuits (Alexander et al. 1986; Cummings 1993).

Increasing synaptic plasticity has been shown to enhance associative motor learning in mice (Jin and Costa 2010), a result consistent with one of the first findings of modern neuroscience. Hebb (1949) formulated the theory that synapses transfer information from one neuron to another, a paradigm that has since guided research on the basic operations of the brain. Synaptic modification is the neural mechanism by which the relations that hold between seemingly unrelated phenomena are learned. The process by which we learn anything – motor acts, words, concepts, etc. – involves modifying synaptic "weights," the degree to which synapses transmit information to a neuron. This is the case for creatures as far removed on the evolutionary scale as humans and mollusks (Carew et al. 1981).

Increased synaptic plasticity and connectivity in the medium spiny neurons of the basal ganglia that resulted from FOXP2 is especially significant in light of their role in associative learning. In combination with dopamine-activated neurons in the basal ganglia and prefrontal cortex, these neurons in essence guide associative learning, coding the expectation of achieving a desired goal or avoiding aversive outcomes (Bar-Gad and Bergman 2001; Joshua et al. 2008; Assad and Eskander 2011). In short, information stored in the synaptic weights of these neurons directs the process of associative learning, allowing animals to learn to perform complex linked sequences. In humans, similar processes account for our learning complex grammatical "rules," as well as the complex "rules" that guide our interactions with other people, other species, and the ever-changing conditions of life.

Other "highly accelerated regions" (HARs) of the human genome may be implicated in neural development (Konopka et al. 2009). These advances in genetics suggest that neural circuits that humans share with other primates were, in effect, "supercharged" by the action of transcriptional genes. Circuits linking prefrontal cortex and the basal ganglia enhance the cognitive and motor capabilities involved in human language and speech. The role of circuits linking cortex and the basal ganglia is well established, but DTI studies reveal a bewildering array of neural circuits in the human brain. We are at the starting point of an understanding of language, cognition, and motor control.

The Archaeological Record

The artifacts preserved in the archaeological record inherently cannot provide direct evidence of their maker's cognitive or linguistic abilities. Computers and software used to write novels represent a technology that is far more complex than Jane Austin's quill pen, yet they do not constitute evidence for a leap in human cognitive ability over the last two centuries. However, there are periods extending over millions of years in which Oldowan tools are virtually identical. Oldowan tools continued to be made by *Homo erectus* as well as hand axes that are more complex, and it is difficult to see how the technique necessary to make them could have been transmitted without some form of language, but they conform to the same pattern over a hundred thousand years. Neanderthal Levallois stone tools are more complex still, and Neanderthals survived in a cold difficult environment. Their brains were as large as humans and they undoubtedly talked. But one signal element that characterizes all human cultures was missing – there is almost no trace of the creative impulse that leads humans to produce art (artifacts that are useless in the struggle for existence that humans produce and value). Nor is there evidence of the pattern of innovation and imitation that mark human behavior in some cultures.

However, the intersection of culture and the biological bases of human cognitive and linguistic ability preclude the archaeological record providing any detailed conclusions on any stage of the evolution of language. In his notebooks, Charles Darwin expressed no doubt that the Yaghan, the indigenous inhabitants of Tierra del Fuego, had the same general cognitive and linguistic capabilities as Europeans (Browne 1995), but he noted the primitive aspects of Yaghan culture. They were naked except for animal skins thrown over their shoulders; later studies found that their tools were similar to those fabricated at Oldowan sites. Yet the three Yaghans who had been brought to England 3 years before on the Beagle had acquired English and conducted themselves in an acceptable early Victorian manner before reverting to Yaghan behavior when they returned to Tierra del Fuego.

Conclusion

The evolution of the biological bases of human language involved natural selection acting on anatomy and neural mechanisms that have a long evolutionary history. Human language did not suddenly arise from a single mutation that occurred 50,000–100,000 years ago, creating an "organ" of the brain – a hypothetical faculty of language – devoted to language and language alone.

The traditional localization of language to Broca's area of the neocortex is also incorrect. Computed tomography (CT) and magnetic resonance (MR) imaging of patients exhibiting aphasia show that damage to subcortical parts of the brain like the basal ganglia, putamen, or olives is necessary to induce permanent loss of language. Neural circuits linking local activity in different neural structures regulate complex behaviors, including speech and language. Circuits linking motor cortex and prefrontal cortex with the basal ganglia play critical roles in motor control including speech, cognitive flexibility, working memory, and other aspects of cognition. Studies of Parkinson, a disease which disrupts basal ganglia operations, have established a relationship between deficits in motor control of internally guided acts and deficits in cognition including language. The basal ganglia constitute a sequencing engine that links internally guided motor acts that control walking, talking, and manual tasks. The basal ganglia also act to interrupt a sequence when changing circumstances suggest a different response. Similar basal ganglia operations involving the basal ganglia linked to prefrontal cortex contribute to cognitive flexibility, the comprehension of distinctions in meaning conveyed by syntax, and tasks such as mental arithmetic. These neural circuits linking cortex and the basal ganglia are not domain-specific, i.e., they are not committed to language and language alone.

Speech plays a critical role in language, permitting information transfer at a rate that exceeds the fusion frequency of the human auditory system. The high data transmission rate of speech involves the process of "encoding," where the individual "phonemes" – roughly equivalent to the letters of the alphabet – are melded together into words. The acoustic signals that convey words are generated by the supralaryngeal vocal tract (SVT), which acts as a variable acoustic filter that produces local energy maxima occurring at *formant frequencies* that are the major determinants of vowel and consonant quality. However, the overall length of a speaker's SVT determines the absolute value of the formant frequencies that conveys a given vowel or consonant. Listeners must form an estimate of the length of the SVT that generated a particular formant frequency pattern to recover the vowel or consonant.

The vowel [i] (the vowel of the word *see*) and to a lesser extent [u] (the vowel of *too*) are optimal signals for recovering the length of a speaker's SVT. Computer-modeling studies and acoustic analyses of the vocalizations of human newborn infants and monkeys and apes show that their SVTs cannot generate these vowels and other "quantal" speech sounds that enhance the robustness of speech communication. Their tongues prevent them from producing the quantal speech sounds that are among the few attested "universals" of human language. Human infants have a tongue situated almost entirely in the oral cavity, more closely resembling the proportions of the tongue in a nonhuman primate or other mammal than that of an adult human. The shape of the adult human tongue is attained through a developmental process involving restructuring of the skull to shorten the length of the oral cavity and descent of the tongue, hyoid, and larynx below the mandible into the neck. This process takes 6–8 years in modern humans. In humans, half the adult tongue is situated in the pharynx in the neck and half is in the oral cavity. Computer-modeling studies show that configuration enables humans to form the SVT shapes necessary to produce quantal sounds.

The evolution of the human tongue can be traced by taking into account the relative length of the oral cavity, which can be determined by examining bony landmarks on the basicrania of fossil hominins and neck length which can be estimated from the dimensions of their cervical vertebrae. Since the tongue carries the larynx down into the neck with it to attain the 1:1 oral to pharyngeal proportions necessary to produce quantal speech sounds, there must be sufficient room for the laryngeal maneuvers involved in swallowing. Taking into account these constraints, Neanderthals and other archaic hominins with a long face and nasopharynx would not have had the 1:1 SVT proportions necessary to produce quantal speech. Speech is, however, possible without the ability to produce quantal sounds. Since the human tongue has a biological liability – increasing the risk of choking on food lodged in a descended larynx – the neural capacity for speech must have been present before the adaptations that yielded the adult humanlike tongue.

The neural circuits that appear to regulate laryngeal phonation appear to have a long evolutionary past, deriving from circuits whose initial purpose was mother–infant communication in transitional mammal-like reptiles. The neural capacity to regulate alveolar (lung) air pressure during speech may also be present in other species. Humans do not appear to have a unique, direct cortical-to-laryngeal neural circuit that confers the ability to learn and execute the motor commands that underlie speech. That seems to be the province of cortical–basal ganglia circuits which in humans are similar to circuits mapped out in nonhuman primates, except that, in the human circuits, synaptic plasticity and dendritic connectivity are enhanced by mutations on the FOXP2 transcriptional gene. Studies of the pattern of deficits of an extended family in which many individuals had only one copy of the FOXP2 gene established the role of the gene in speech motor control, cognition, and language. Comparisons of DNA from chimpanzees, contemporary humans, and fossil DNA recovered from Neanderthals and Denisovans revealed distinctions between the forms of FOXP2 in chimpanzees, Neanderthals, and humans. A series of selective sweeps, the most recent at about 260 ky ago, occurred on the uniquely human form of FOXP2. Other transcriptional genes are most likely implicated in evolution of the neural capacities that confer human cognitive and linguistic ability.

Darwin pointed out that biological evolution and the ecosystem, which for humans includes their culture, are not separable. Selective sweeps for adult lactose tolerance, for example, occurred in cultural settings in which milk-producing animals were domesticated. This argues against the universal grammar (UG), proposed by Chomsky, which specifies the details of syntax and the sound pattern of every language. The UG is necessary for a child to acquire any language. If such were the case, natural selection and selective sweeps would have occurred to optimize UG for the language spoken in a particular culture, rendering it deficient for acquiring languages that differed. However, a child from any cultural background can learn any language with native proficiency if he or she is immersed in a given culture at an early age. Likewise, chimpanzees raised in a human setting where sign language is used can, to a degree, learn to use words and understand simple syntax – demonstrating the continuity of the evolution of human language and the antiquity of some of the elements that constitute language.

Cross-References

▶ Ancient DNA
▶ Cooperation, Coalition, Alliances
▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
▶ Evolution of the Primate Brain
▶ Hominoid Cranial Diversity and Adaptation
▶ Modeling the Past: Archaeology
▶ Neanderthals and Their Contemporaries
▶ Origin of Modern Humans
▶ Paleoecology: An Adequate Window on the Past?
▶ Primate Intelligence

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General Principles of Evolutionary Morphology

Gabriele A. Macho

Contents

Abstract

Anthropologists analyzing morphology for phylogenetic, functional, or behavioral purposes are confronted by a plethora of obstacles. Morphology is not free to vary but is subject to a number of constraints, which may be historical, developmental, and/or functional, while equivalency in function can be achieved by different means. This, together with the fact that the fossil record is scant, confounds meaningful interpretation of phylogenetic pathways and the reconstruction of function and behavior from fossilized remains. To overcome these difficulties, paleoanthropology is becoming increasingly inter- and multidisciplinary, whereby researchers draw on, and incorporate, approaches and findings obtained in other, sometimes very diverse, disciplines. This contribution briefly reviews the constraints acting on morphology, the limitations faced when interpreting form/function and behavior from morphology, and the different approaches currently explored in paleoanthropology to obtain a better

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G.A. Macho (✉)
Research Laboratory for Archaeology (RLAHA), University of Oxford, Oxford, England
e-mail: gabriele.macho@rlaha.ox.ac.uk; gabriele.a.macho@gmail.com

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understanding of hominin paleobiology. While offering exciting new possibilities, researchers should however be mindful of the limitations inherent in new technologies.

Introduction

With rare exceptions (e.g., endocasts, footprints, permafrost remains, peat bodies), only the hard tissues of the body become fossilized. Phylogenetic, functional, and behavioral interpretations of extinct taxa are thus almost exclusively based on analyses of bones and teeth. Yet, fossil remains are mostly incomplete and distorted, while taphonomic biases prevent a good representation of all parts of the body and/or functional units for detailed analyses (chapter "▶ *Homo ergaster* and Its Contemporaries," Vol. 3). It is therefore unsurprising that the search for more fossil material is a priority in paleoanthropology. These shortcomings aside, there exist other more fundamental problems in analyzing and interpreting morphology. Resolving these issues is the aim of diverse research areas, whose integration has only just begun.

Morphology is highly constrained and determined by a cascade of interactions between genetic, epigenetic, and environmental factors modulated through past and present selective pressures. Consequently, morphology and function must not only be interpreted with respect to present-day function and the fitness it confers to the species but should also be viewed against the backdrop of past form, function, and selective pressures. Phenotypic correlations due to pleiotropy, epigenetics or correlated selection, genetic drift, and co-option of characters for functions that were not initially selected for compound appraisals of morphology within a phylogenetic and functional framework. The fact that developmental pathways for various structures are only poorly (if at all) understood complicates this endeavor even further. Questions as to whether form followed function or whether it was the reverse largely remain unanswered. This is problematic though, as speciation is commonly associated with the acquisition of novel morphological characters and/or the exploitation of new ecological niches. Resolving form/function relationships is thus pivotal for evolutionary inquiry.

To overcome problems associated with the interpretation of morphological structures and variation in both extant and extinct populations, evolutionary studies have become increasingly multi- and interdisciplinary. Traditional comparative approaches prevail, but two main strands of distinct research lines have started to emerge. First, evolutionary developmental biology, despite its long (and sometimes misguided) history (Haeckel 1866), is now a well-established discipline (Hall 1992). Such studies combine an experimental, developmental research protocol with comparative analyses of the fossil record in order to determine the developmental and phylogenetic pathways of morphological structures and the constraints acting on their formation. Despite their high power of resolution, experimental developmental studies are not part of mainstream paleoanthropological inquiry: they require specialized knowledge, are time consuming, and are financially costly.

Second, new comparative, functional, and biomechanical tools are increasingly incorporated in paleoanthropological research protocols and have made, and continue to make, a valuable contribution to our understanding of the functional adaptations of extinct species.

A comprehensive review of the various strands of inquiry is beyond the scope of this contribution. Instead, this chapter aims to highlight some of the general problems and limitations associated with interpreting the morphology of fossil remains and when employing new technology.

Comparative Morphology and Constraints

Morphology is not free to vary but is subject to a number of developmental, physical, and historical constraints (Maynard Smith et al. 1985), while, except for more recent hominins like Neanderthals, for example (Green et al. 2010), genetic information is not available and identification of constraints relies exclusively on comparative analyses of hard tissue remains. This limits what can be learned about the paleobiology of our ancestors.

Comparative Morphology and Evolutionary Constraints

Phylogenetic systematics or cladistics is the main tool for reconstructing the phylogenetic relationships of taxa (Hennig 1966) and should precede paleobiological inquiry and functional analyses (Felsenstein 1985; Harvey and Pagel 1991). While the strengths and weaknesses of this method, as well as its assumptions, are reviewed elsewhere in this handbook (chapters "▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns," Vol. 1, "▶ The Biotic Environments of the Late Miocene Hominoids," Vol. 2 and "▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins," Vol. 3), some limitations pertaining to the analysis and interpretation of morphology need to be briefly reiterated. Relevant for the discussion of constraints are issues regarding homology and the independence of characters. Analyses of homologous traits are at the heart of cladistic methodology, but experimental studies have provided unequivocal evidence for the hierarchical nature of homology, whereby homologies at one level of organization need not lead to homologies at another (Hall 1994); in fact, Hall (2007) argued for homology and homoplasy to be viewed as opposite extremes of a continuum only. This seems justified as anatomical traits are not independent, but result from pleiotropy, correlated selection, modular networks, and genetic linkage. Although this arguably obscures the elucidation of the phylogenetic history of taxa and hampers inferences about the relationships between form, function, and behavior, such correlations are themselves useful and provide meaningful insights into the evolvability of complex systems (e.g., Marroig et al. 2009), i.e., the tempo and mode of evolution. Unsurprisingly thus, the study of covariances has experienced a renaissance in recent years (Olson 2012).

On the basis of methodologies originally developed in population genetics, various quantitative tests have been employed to appraise the covariations and correlations of traits with the aim of inferring developmental and phylogenetic constraints (Cheverud et al. 1989). In the last few years, paleoanthropology has seen a boom in the application of this approach, aided by the affordability of powerful computers and mathematical advances, such as geometric morphometrics (Bookstein 1991). Investigations tend to focus on serially homologous structures, like hominoid limbs (Rolian et al. 2010; Young et al. 2010) and teeth (Hlusko et al. 2004), and on developmentally and/or functionally integrated (and complex) systems, such as the skull and mandible (Ackermann 2009; Lieberman et al. 2000, 2004; Zelditch et al. 2009) and the pelvis (Grabowski et al. 2011). An understanding of the integration and modularity of various structures is starting to emerge, including their potential for evolutionary change, i.e., evolvability, and the rate at which these changes can occur during evolution. For example, Hlusko et al. (2004) estimated that enamel thickness in baboons could theoretically double in only 50,000 generations. If correct, this character would be prone to homoplasy, and enamel thickness as a defining trait in hominins should be interpreted with caution. Also, the low levels of integration found in the pelvis (Grabowski et al. 2011; Lewton 2012) are likely to underlie both the rapid evolution of bipedality and the diversity of locomotor patterns among hominins (e.g., DeSilva et al. 2013).

Comparative Morphology and Functional Constraints

Comparative studies are at the heart of paleoanthropology, even though hominins do not have a modern analog and have adapted to their environment in unique ways, both behaviorally and morphologically. Unfortunately, natural experiments which directly inform hominin evolution are rare. The only exception is perhaps chapter "▶ *Homo floresiensis*," Vol. 3 (Brown et al. 2004), whose diminutive size and small brain continues to be subject of study (Kubo et al. 2013). While the species' taxonomic affiliation remains unresolved, most researchers view the unique morphology of *H. floresiensis* as a typical response to the environmental conditions encountered on islands, i.e., resource limitations and lack of natural predators (chapter "▶ The Species and Diversity of Australopiths," Vol. 3). For other hominins the link between environment and morphology is far less obvious and inferences are derived predominantly from analyses of hard tissue remains.

Teeth

Teeth are among the most abundant remains within the fossil record and contain a wealth of information for the taxonomists and functional morphologist (chapter "▶ Modeling the Past: The Paleoethnological Approach," Vol. 1). Owing to their pivotal role in the breakdown of food (Strait 1997), overall size, shape, and enamel thickness are considered good indicators of the dietary niches exploited by extinct species (Janis and Fortelius 1988); when analyzed across lineages and clades with specialized diets, they even provide information about global climatic fluctuations

(Fortelius et al. 2002). The importance of tooth morphology for functional inferences is thus undisputed, but the high level of homoplasy compromises the usefulness of teeth for taxonomic purposes. For example, the hypocone probably evolved independently more than 20 times (Hunter and Jernvall 1995), while thick enamel among primates could be the result of convergent evolution also (Janis and Fortelius 1988; Hlusko et al. 2004). For a functional assessment the most useful, yet underexploited, feature is the way in which dental material, particularly the hard and brittle enamel, is strengthened to prevent the propagation of cracks (Rensberger 2000). Structural strengthening is achieved through enamel decussation, which has evolved in large-bodied taxa and those that employ high bite forces (von Koenigswald et al. 1987). Although attempts have been made to deduce prism decussation from their optical manifestations, i.e., the Hunter-Schreger, these optical phenomena do not adequately capture the levels of decussation in primates.

Prismatic enamel is a characteristic trait of Eutheria: it is brought about by the movement of ameloblasts from the dentinoenamel junction to the outer enamel surface during ontogeny and the differential orientation of hydroxyapatite crystals within the prism heads and its surrounding matrix (Boyde 1989; Osborn 1981). As the undulating prisms of one layer are (usually) offset with regard to layers of prisms above and below them (Fig. 1), bundles of prisms (crystals) will not be aligned in parallel, but will be angled in relation to each other. This apparent "crossing-over" provides a powerful crack-stopping mechanism (Rensberger 2000; von Koenigswald et al. 1987). This is because cracks tend to travel along the prism boundaries, i.e., the protein-rich prism sheaths (Fig. 1). Prism boundaries constitute the path of least resistance, whereas considerably more energy is required for a crack to traverse the strong hydroxyapatite crystals (Boyde 1989). By aligning prisms/crystals at angles relative to each other, cracks initiated while biting or through external forces, e.g., a blow to the head, will be stopped and crack propagation and catastrophic tooth failure will be prevented (except in rare circumstances). Differences in enamel prism organization thus hold information about the loading conditions habitually encountered by a species but also about wear resistance. As a case in point, the angles at which prisms intersect the wear surfaces will affect the rate at which the tissue is worn (Shimizu et al. 2005), an information that can be used to appraise whether the thick enamel of hominins is indeed an adaptation to wear resistance, as often conjectured (Macho and Shimizu 2009). Evidently thus, enamel microanatomy provides a wealth of information for an understanding of the ecological niches of hominins, but quantification of these differences remains difficult. Enamel is dense and chemically homogenous such that structural differences are achieved solely by the different orientations of hydroxyapatite crystals/prisms. The means to retrieve microanatomical details are therefore limited and include serial sectioning of the tissue (Hanaizumi et al. 1998; Osborn 1968), using high-resolution specialized imaging techniques such as the synchrotron (Tafforeau et al. 2012), or reconstructing the prism undulations from naturally broken surfaces (Macho et al. 2003; Macho 2004; Jiang et al. 2003). Despite the relative paucity of data resulting from these difficulties, however, it is clear that prism decussation is the combined outcome of prism undulation in

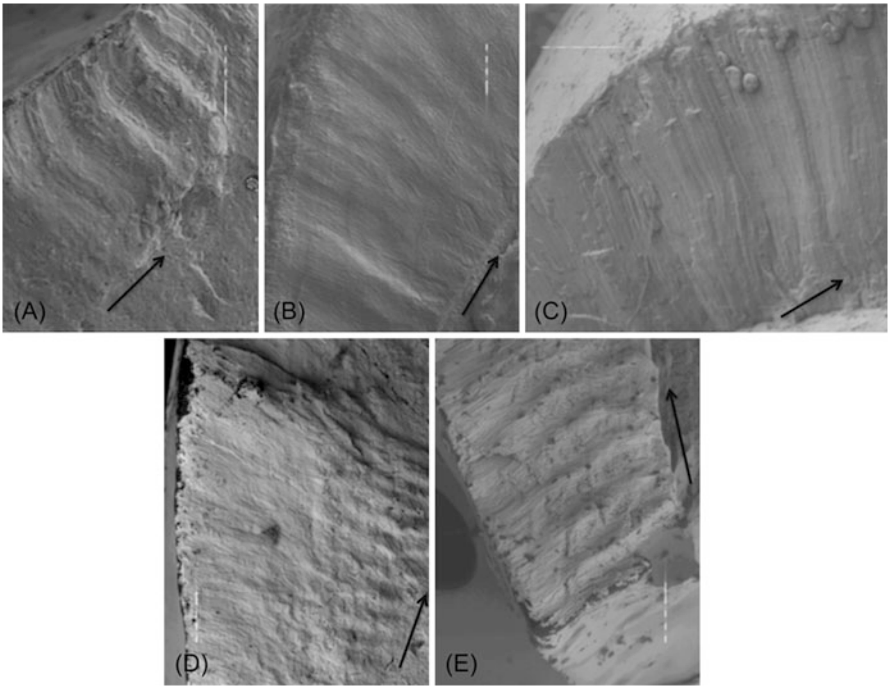

Fig. 1 Scanning electron microscope images (SEM) of naturally broken enamel structures of hominin teeth. (**a**) *Australopithecus afarensis* (LH6, I), (**b**) *Kenyanthropus platyops* (WT38356, RM1/2), (**c**) *Paranthropus boisei* (OH30, RM1), (**d**) *Australopithecus africanus* (Stw208, RM1), and (**e**) early *Homo* from Swartkrans, South Africa (SKX269, RC). *Arrows* are placed at the dentinoenamel junction and point toward the cusp tip; note that the *arrow* for *P. boisei* is directed slightly into the enamel to indicate that the break for this specimen, as for most *P. boisei* specimens, is somewhat oblique. For *A. afarensis* (**a**) and early *Homo* (**e**), images are from more cervical regions, thus explaining the thinner enamel; all other images are from mid-crown levels. Prism undulations are species-specific and levels of decussation vary substantially from high (**e**) to low (**c**)

3D space and the rate at which prism paths are offset in relation to each other apico-cervically. This appears a simple mechanism, yet it suffices to yield remarkably different patterns among closely related hominins (Fig. 1). The biomechanical consequences of these differences are significant too and are not anticipated from analyses of external morphology alone (Macho and Shimizu 2010; Shimizu and Macho 2008). Functional interpretations and dietary inferences based on overall tooth morphology, including enamel thickness, should therefore be viewed cautiously.

Bone

Unlike enamel, bone is a plastic material and continues to remodel throughout life in response to loads placed on it (Wolff 1892; for review see Pearson and Lieberman 2004; Ruff et al. 2006). Not all aspects of bone are equally informative as to their function in vivo (Currey 2002). Joints have evolved to confer both optimal orientation with regard to the direction of load and mobility, although the relative contribution of each of these aspects, as well as the magnitude of loads, remains uncertain. Until recently, the study of joint surfaces has been relatively neglected in paleoanthropology. With the affordability of more powerful computers and with advances in capturing and analyzing complex 3D shapes, this has begun to change (Parr et al. 2011; Tocheri et al. 2007). Analyses of joint surfaces is likely to become an important aspect of functional studies, especially when combined with an assessment of the subchondral bone densities underlying these surfaces (Carlson and Patel 2006; Nowak et al. 2010). Weight-bearing bones (e.g., vertebrae, calcaneus) or weight-bearing aspects of long bones (i.e., proximal ends) gain their structural stability through a meshwork of interconnected trabeculae. Such an arrangement ensures maximum strength while, at the same time, minimizing weight; unsurprisingly 70 % of all the bone is thus trabecular bone (Huiskes 2000). In order to optimize the functional adaptations of bone, trabeculae tend to align along the principal stress trajectories (Abel and Macho 2011; Biewener et al. 1996).

In an innovative comparative study, Ruff et al. (1994) investigated the response of bone remodeling during different stages of ontogeny. They found that increased mechanical loading prior to (or during) adolescence leads to an increase of cortical bone thickness due to periosteal expansion. Conversely, increased loading during later stages of development results in endosteal contraction with external diameters remaining relatively unaltered (Ruff et al. 1994). In addition, cortical bone responds systemically to increased activity levels during ontogeny, even in the absence of direct loading (Lieberman 1996). Increase in bone length, in contrast, is largely stimulated through the effects of growth hormone at the growth plates and indirectly through muscle action (Vogl et al. 1993). Taken together thus, physical activity during development, i.e., during adolescence in particular, will have the greatest effect on bone remodeling through direct and indirect stimulation, whereas activity levels during adulthood will result in comparatively minor changes. With these provisos in mind, activity levels, particular behaviors, and the timing of their onset can be deduced from cortical bone thickness and cross-sectional shapes in archaeological samples and fossil hominins (e.g., Stock 2006). What has thus far been underappreciated in paleoanthropological studies is the potential importance of collagen fiber orientation within the bone matrix, its response to loading and its significance for functional interpretations (McFarlin et al. 2008; Skedros et al. 2011). Like enamel, bone is a structured hierarchical material, whose consequences for mechanical behavior and abilities to absorb and/or distribute loads may be more significant than anticipated from gross anatomy alone (Bechtle et al. 2010) (Fig. 2).

Trabecular alignment within bones similarly responds to loading. Although the main trajectories are developed relatively early during development (Biewener et al. 1996; Tanck et al. 2001), trabeculae continue to grow differentially in areas where strengthening is needed and are resorbed where it is not (Abel and Macho 2011; Biewener et al. 1996; Tanck et al. 2001; Frost 1990; Kobayashi et al. 2003).

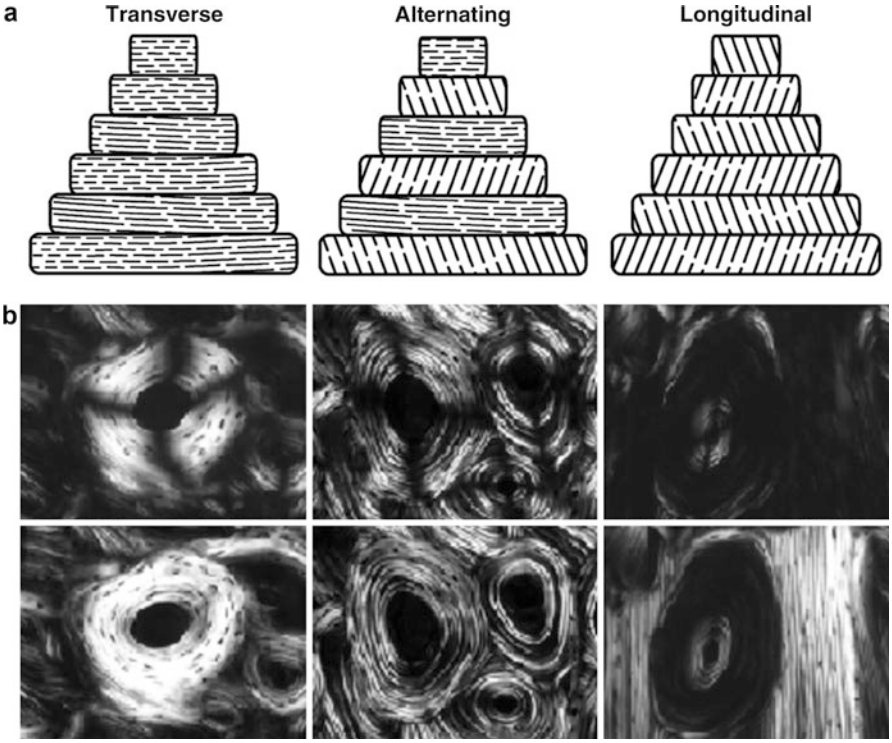

Fig. 2 (**a**) Illustration of the predominant collagen fiber orientation patterns of osteons and (**b**) their appearance in histological sections, i.e., linearly polarized light (*top*) and circularly polarized light (*bottom*) (Adapted from Skedros et al. (2011) and Bromage et al. (2003) with permission)

The potential of trabeculae for (re)modeling later in life offers exciting possibilities for anthropological inquiry. That is, when viewed against overall bone shape, which tends to be phylogenetically and ontogenetically more constrained, trabecular architecture is a better indicator of an animal's behavior in vivo than gross morphology. Combined analyses of external and internal morphology therefore shed light on fundamental questions in paleoanthropology, e.g., whether a primitive morphology constitutes a plesiomorphic character (phylogenetic constraint), whether it has been retained by stabilizing selection (behavior), or whether it has simply not been selected against (phylogenetic inertia) (Ward et al. 2001). These possibilities were recently explored for the capitate of *Australopithecus anamensis* and *A. cf. afarensis* (Macho et al. 2011). Carpals and tarsals are particularly useful when addressing such questions: they lack epiphyseal plates and, with some rare exceptions, muscles attachments (Bryant and Simpson 1984; Dainton and Macho 1999a, b). Consequently, their development is influenced less by hormones and muscle pull, while the internal bony architecture will directly reflect the loading conditions encountered (Fig. 3).

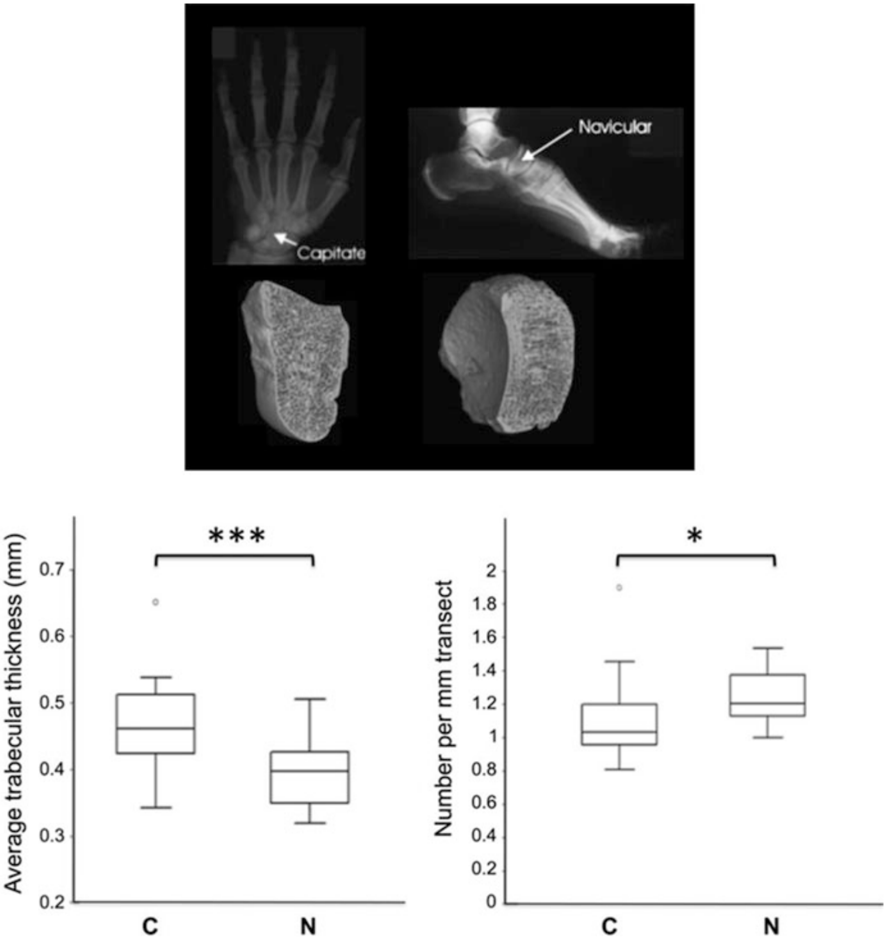

Fig. 3 Systematic differences in isotropy, trabecular thickness, and density between weight-bearing (navicular) and nonweight-bearing (capitate) bones in modern humans (Adapted from Macho et al. 2005). *C* capitate, *N* navicular; asterisks indicate significance levels using paired *t*-tests

Determination of Functional Adaptations

Adaptations are traits which enhance the fitness of the species and have arisen over evolutionary time as a result of natural selection for present biological roles (Rose and Lauder 1996). Inferring the functional adaptations is not trivial even when the traits under investigation do not constitute evolutionary novelties. Comparative analyses based on analogy with extant taxa assume that structure and function are intricately linked, but this is seldom the case (Lauder 1997). Importantly, most biological structures have evolved to fulfill more than one function and many complex systems are mechanically redundant: similar outcomes can be achieved through different means, as shown for the masticatory apparatus, for example (Koolstra 2002). From an evolutionary perspective, redundancy is advantageous, because it increases a structure's evolvability (Wainwright et al. 2005), but for the paleoanthropologist it is troublesome, because it reduces the confidence with which function can be inferred from morphology.

Traits which are advantageous and enhance the fitness of the species may in fact have evolved for a different purpose or they could initially have been the result of random genetic drift, pleiotropy, or correlation with other structures (Gould and Lewontin 1979; Gould and Vrba 1982). Until recently, exaptations have been assumed to be rare, especially in hominins. Two possible exaptations have now been identified: the crack-stopping morphology of the dentine-enamel interface (Shimizu and Macho 2007) and hominin finger proportions which then facilitated the emergence of stone tool technology (Rolian et al. 2010). In order to affirm that evolution has selected for a certain trait, it is imperative that extant analogs exist and that the function is similar in all living species. Inferences about functional adaptations thus formulated should then be supported by biomechanical analyses. Additionally, the first appearance of the feature must be found to coincide with (and be supported by) ecological and environmental evidence, for which the feature and its functional adaptation had apparently been selected (Lauder 1982; Anthony and Kay 1993). Hominin morphology should therefore always be interpreted within the ecological and environmental settings of that species (Vrba et al. 1995; Bromage and Schrenk 1999). On theoretical grounds the procedure for identifying functional adaptations is straightforward but, in reality, it is challenging: the hominin lineage contains only one extant taxon, *Homo sapiens*; the fossil record is incomplete; experimental data on extant species are scarce; and there is much to learn about the environment in which early hominins evolved (chapters "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence," Vol. 2 and "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). To overcome some of these limitations, sophisticated experimental tools are now routinely used in paleoanthropology, particularly finite element stress analysis (FESA). This method is well suited to determine the functional constraints of morphologies, provided the limitations and assumptions underlying model creation are borne in mind.

The usefulness of FESA for (paleo)anthropological inquiry was first explored over a decade ago (Macho and Spears 1999; Spears and Macho 1998), and this method has now become part of the mainstream paleoanthropological tool kit (e.g., Ross 2005). FESA is a numerical modeling technique that examines the deformation of a virtual model composed of a meshwork of elements with given material properties, such as elasticity (Young's modulus), Poisson's ratio (the change in width after a given change in length), shear properties (shear modulus), density, bone mineral fraction, etc. (see Rayfield 2007 for a simplified review of the principles of FESA and applications in paleontology). This technique is particularly useful where an assessment of the internal mechanical behavior of structures is sought and/or where noninvasive approaches are required, as is the case for hominin fossils. However, FESA is not without pitfalls. Perhaps most crucial for an assessment of the functional adaptations (apart from overall geometry) is the input of material properties. Both teeth and bone are highly complex hierarchical structures (Figs. 1 and 2). Unfortunately, computer capacities are limited and only a finite number of details can be inputted. Put simply, the larger the structure under investigation, the cruder the model. Although efforts are being made to improve the input parameters and diversity of material properties used, many more improvements are necessary when dealing with large complex objects, like the primate skull. As a case in point, to create the complexity of the entire skull, Strait et al. (2010) used some 311,000 (macaque) and 778,000 (*Australopithecus africanus*) elements. In contrast, the average number of elements used to represent a small block of enamel was 440,000 (Macho et al. 2005; Macho and Shimizu 2010). Despite the apparently high level of detail, these enamel models are still simplifications though: the protein-rich prism sheaths separating enamel prisms were not modeled, although their biomechanical significance is undisputed (Ge et al. 2005). Inputting these data would have surpassed the computational capabilities. Deciding on the boundary conditions, i.e., the loads and constraints placed on the models, is another problematic area and a potential source for misleading results, particularly when investigating complex systems. For example, the masticatory system is redundant (Koolstra 2002) and the mandibular stroke varies within and between individuals depending on the size and properties of food, age, individual preference, pathology, muscle physiology, motor control, etc. (Woda et al. 2006). Deciding on the bite direction is therefore difficult, even more so when dealing with extinct taxa that are represented by incomplete skulls only. This is important, as the orientation of the applied load, and the locations of restraints, i.e., where the model was fixed, will significantly affect the stress flow within that structure. This highlights that while engineering techniques provide powerful and useful tools for functional analyses, models are only as good as the data inputted and the assumptions made.

Determination of Behavior

Determination of behavior is probably the most difficult and contentious aspect of anthropological inquiry. The correspondence between morphology, performance, and behavior is generally inadequate (Lauder 1997). Behavioral inferences largely rest on comparative approaches aiming to deduce the biological role of morphology (bone and tooth size and shape, muscle markings, etc.) from modern analogs. But fossil species are unique: they do not have modern analogs. What is more, the farther back in time, the more fragmented the hominin fossil record becomes with associated partial skeletons being extremely rare (Berger et al. 2010; Johanson et al. 1982, 1987; Toussaint et al. 2003; Walker and Leakey 1993; White et al. 2009). Reconstruction of the bony elements therefore relies on the expertise of the morphologist working with comparative material and/or composite constructs; morphological differences between individuals, as well as temporal changes in morphology, can become obscured.

The fact that a species was capable of performing certain functions and behaviors does not necessarily imply that it habitually did do so. Both modeling and biomechanical analyses can only determine the boundary conditions, i.e., constraints, of morphological structures and infer their *potential* capabilities. A distinction must be made between what a species *could* do and what it *did* do. An animal's behavior is contingent on many factors other than morphology, such as the environment, competition among sympatric species, resource limitations, etc. The evolutionary success of a species will ultimately depend on how it negotiates the challenges and vicissitudes posed by the biotic and abiotic environment within the confines of its own biology. It will be challenging for the paleoanthropologist to separate these aspects. Among hominoids, for example, sympatric *Pan* and *Gorilla* feed on the same fruits during the fruiting season, but food selection changes more dramatically among gorillas than chimpanzees during the dry season (Kuroda et al. 1996). Similar scenarios are possible for sympatric hominins, e.g., *Homo* and *Paranthropus*.

Conclusions

Fossil remains of hard tissue, such as teeth and bones, provide a wealth of information for the evolutionary biologist aiming to reconstruct the phylogenetic history and functional adaptations of extinct species. Unfortunately, disentangling these various aspects is not trivial and requires that paleoanthropologists employ a number of analytical tools, draw on information obtained in other disciplines (i.e., behavioral, developmental, and experimental), and collaborate with researchers in other areas. It has become abundantly clear that no single approach or technique suffices to shed light on the functional adaptations and behaviors of extinct hominins. At the same time each technique has inherent limitations and is built on assumptions that cannot always be overcome. Choosing the appropriate research tools and bearing in mind limitations specific to each approach is essential when interpreting the results. Nonetheless, the increasingly multi- and interdisciplinary nature of paleoanthropological research has much to offer and has begun to generate new and exciting (as well as partially testable) hypotheses at a faster rate than ever before. Given that hominins are large-brained primates that display behavioral flexibility and dietary selectivity, it is perhaps prudent not to ask what they did do but rather what they were incapable of doing. By turning the fundamental question about form, function, and behavior of extinct hominins around, better insights into the evolutionary biology of our lineage can be gained.

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Virtual Anthropology and Biomechanics

Gerhard W. Weber

Contents

Abstract

The scarcity of fossil hominins imposes the obligation to extract as much information as possible from the few existing remains. Virtual anthropology exploits digital technologies in an interdisciplinary framework to study the morphology of specimens in 3D and 4D. It can contribute to this aim because structures are easily accessible, powerful morphometric analyses can inform about intragroup and between-group form and shape variation, data manipulations and reconstructions become more reproducible, and sample sizes can be increased via sharing of electronic data. The six main areas of virtual anthropology – digitize, expose, compare, reconstruct, materialize, and share – are introduced in this chapter. Biomechanics on the other hand allows inferring certain aspects of function via the study of loadings in structures. Though an

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G.W. Weber (✉)
Department of Anthropology, University of Vienna, Wien, Austria
e-mail: gerhard.weber@univie.ac.at

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efficient formal bridge between those two domains is still missing, there are many overlaps and cross-fertilizations visible, possibly leading into a “virtual functional morphology” to better understand evolutionary adaptations.

Introduction

When the first hominin fossil (later classified as Neanderthal) was found in 1829 by P.C. Schmerling at Engis/Belgium and described by him soon thereafter (1833), there was no such science as paleoanthropology. Not even a proper idea of evolution had been formulated by then, though it was spooking in the head of some enlightened already. This comes as no surprise since the appreciation of human evolution just makes sense if one accepts the changeableness of species and populations – a frightening idea for some against the safe harbor of religious beliefs.

Schmerling recognized that the fossil remains he found were different from what he knew as anatomist and would belong to a “primitive species” (1833, p. 124). Though he was, e.g., impressed by the size of teeth, he had of course no good means to capture size and shape quantitatively to be compared against other populations. T. H. Huxley later used (1863) Engis and the famous calotte from the Neanderthal to argue for Darwin’s ideas. Today, in the second decade of the twenty-first century, we have developed a great many of machines and methods to extract information of all kinds from fossil material so that the approaches of the nineteenth century – describing form mainly qualitatively or adding only a few quantitative measurements – are becoming more rare.

Paleoanthropology tries to settle questions (Henke 2007) like what distinguishes us from our next living relatives, when and where did humans branch off from the other primate tree, which ecological framework enabled the process of becoming human, how many and which hominins were out there, and how did we develop our specific traits like bipedal locomotion or language? The main challenge in our science is that there are only so few sources of evidence available to answer these questions. And even if the number of discovered fossils has increased impressively in the last few decades, we cannot nearly hope to close the gaps in the record or collect representative sample sizes. In the evolutionary sciences, we can only model populations and processes with more or less confidence.

This scarcity of material imposes the obligation to extract as much information as possible from the few existing remains. We have to think hard about experimental designs, methods, and collaborations with other sciences to match this claim. Who would have thought 50 years ago that we would have the complete sequence of the Neanderthal genome (Prüfer et al. 2014) or that the shape of the tiny semicircular canals in the inner ear (Hublin et al. 1996) would suggest a species assignment? If we consider paleoanthropology as a part of the natural sciences (Tattersall and Schwartz 2002), on the other hand we need to follow its rules, i.e., *that explanations must come from observations that can be repeated and confirmed by other researchers*. This requires eliminating subjective opinions and irreproducible results. Otherwise paleoanthropology is indeed nothing else than a narrative science – a story telling in the sense of Landau (1984). Consequently, we have to walk the thin line between exploiting every possible bit of information stored in a fossil, but not exaggerating its interpretation and keeping in mind the uncertainty that comes attached to our data. Darwin himself recognized the poisonous influence of erroneous data (1871, vol. II, p. 385): "False facts are highly injurious to the progress of science, for they often long endure; but false views, if supported by some evidence, do little harm, as every one takes a salutary pleasure in proving their falseness; . . .."

Quantitative data and computer environments offer the advantage that every manipulation becomes obvious, at least it can be made public, if that is the intention. In this sense, virtual anthropology and also biomechanical simulations have the potential to make a step toward reproducibility and, of course, toward sharing ideas and data with the speed of light. This does not guarantee proper investigations. The machines and algorithms will only produce results as intelligent as the researcher has designed the analyses. Critical reflection is important and necessary. T. White put it to the extreme when he said in his Millennium essay (2000, p. 288): "The careerist leaps on each passing technological bandwagon. [. . .] Results can be instant, irreproducible, and irrelevant. When applied without appropriate biological background, they simply muddle fundamental issues in human evolution." We have indeed to take care that methods and machines are used advisedly and that researchers understand the prerequisites and limits of their use. However, there are enough documents in support of useful applications out there and also White and colleagues later used the toolkit of virtual anthropology to describe and analyze their fossils (e.g., Suwa et al. 2009).

Virtual anthropology (VA) exploits digital technologies and pools experts from different domains such as anthropology, paleontology, primatology, medicine, mathematics, statistics, computer science, and engineering. VA, as the author here defines it, deals mainly with the functional morphology of recent and fossil hominoids. Its methods can, of course, be applied in a much broader sense, e.g., for other primates, mammals, vertebrates and invertebrates, and even for plants or tools. The term "virtual anthropology" was coined in the mid-1990s and first published in 1998 (Weber et al. 1998) when computer power and software became available to work reasonably with digital 3D data – though still at enormous expenses. The term is just one of several (e.g., computer-assisted paleoanthropology; Zollikofer et al. 1998) to mark the onset of a new approach in the field of biological anthropology – performing morphological analysis by means of digital data in a computer environment. Many people have contributed to pioneer this field, e.g., Fleagle and Simons (1982) using computed tomography (CT) to study long bones of an Oligocene primate; Wind (1984) investigating the famous Pithecanthropus IV fossil from Java; G. Conroy and M. Vannier with their first attempt to electronically remove matrix from a fossil scan to investigate the cranial cavity (Conroy and Vannier 1984), and a little later (1987) to determine the dental development of the Taung child; Spoor et al. (1994) revealing inner secrets of the bony labyrinth; and Zollikofer and colleagues (1995) virtually reconstructing

Neanderthals and other fossils. The first paleontologist using radiological methods to study hominin fossils, though not digitally, was D. Gorjanovic-Kramberger who published on inner details of the Krapina material (1902) only 7 years after W. Röntgen's discovery of X-rays. For a more comprehensive history of the field, see, e.g., Spoor et al. (2000) or Weber and Bookstein (2011a).

In modern paleoanthropology it is beyond any discussion to use the merits of machine power and simulations. But what did we gain after all? Based on the most striking differences to traditional approaches, namely, that virtual copies are used (which derive from digitization processes such as computed tomography or surface scanning, see below) and that these data can easily be analyzed in 3D or 4D within a computer environment, some crucial advantages resulted:

1. The accessibility of the *entire* structure, including usually *hidden features*, e.g., the braincase, the sinuses, the dentin of teeth, the medullary cavities of long bones, or the heart including its chambers.
2. The *permanent* availability of virtual objects (24/7) on hard drives or servers.
3. The possibility of obtaining a dense mesh of measurements across the whole geometry for *powerful* quantitative analyses of form and function.
4. The great range of options for data handling, statistics, visualization, and data exchange for increasing sample size.
5. The increased reproducibility of procedures and measurements, a fundamental requirement of science, as mentioned above.

It is noteworthy to say that the approach is not restricted to questions in paleoanthropology, though this is the main focus of the current article. Medical applications and comparable studies on living primates have arisen (see below), and tools and artifacts can be analyzed in the same manner (cf. Weber 2013). Talking about fossils, however, needs some extra words on the limitations. Although a fossil appears to be a simple static object, a piece of stone of some specific shape, it may convey a rich variety of data, for instance, with regard to macroanatomy (e.g., the shape of the cranial vault, jaw, or teeth), microanatomy (e.g., the orientation of trabecular structures or the prisms of dental enamel), taphonomy (e.g., the degree of mineralization, the presence of cut marks), individual life history (e.g., traumata and pathologies, incorporated trace elements), or perhaps genetics (ancient DNA from cell mitochondria or nucleus). A virtual fossil currently only contains a small fraction of this information, mostly concerning macroanatomy (and occasionally, depending on the resolution, microanatomy), and probably taphonomy and life history. In the case of volume data, e.g., CT, there is no color or texture information. In the case of surface data, there is information on texture and color together with the digitized surface, but there are no internal structures beneath the surface. Other data channels are missing entirely most often, for instance, a virtual fossil usually does not provide any information on DNA or trace elements. Virtual fossils are thus *not intended as a substitute* for real fossils. They are useful for specific purposes only: to work on all kinds of aspects with regard to shape and form of the whole structure or its parts. And it is advisable in many cases to look at the original or a

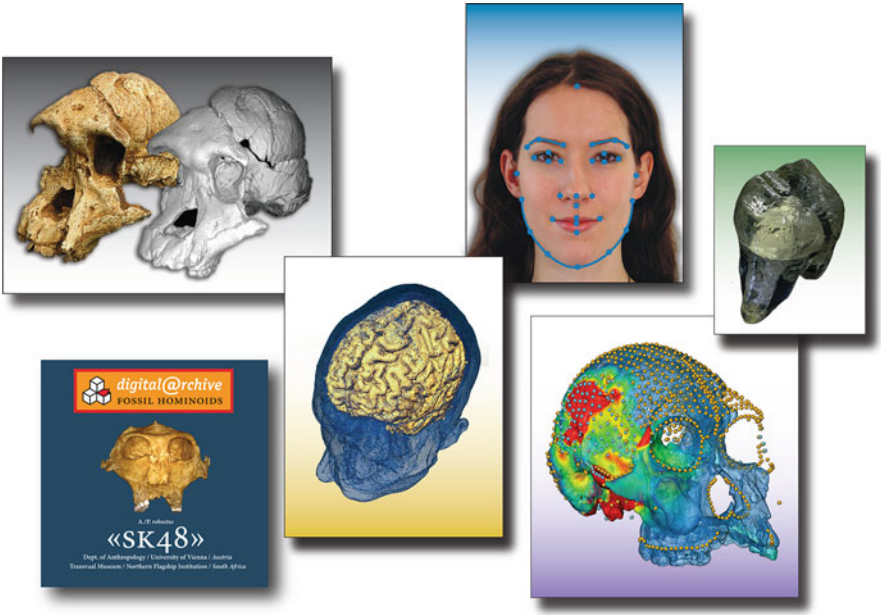


Fig. 1 The six operational areas of virtual anthropology: Digitize (*top left*) – an original specimen and its virtual copy (Stw 505). Compare (*top middle*) – landmarks and curves to capture the shape of a face. Materialize (*top right*) – upscaled transparent stereolithographic model of an australopithecine tooth (Photo by R. Ginner). Share (*bottom left*) – example CD-ROM from the digital@rchive of fossil hominoids. Expose (*bottom middle*) – Magnetic Resonance Tomography, segmented brain, and transparent head. Reconstruct (*bottom right*) – undeforming parts of an australopithecine skull using reference data (Sts 71, reconstruction by P. Gunz)

premium cast during work since our senses are not well adapted to rely on screen simulations only.

While virtual anthropology was quite an exclusive endeavor in the 1990s, today the demands fall within the feasible range of a medium-cost lab. The most typical infrastructural and personal requirements for a VA lab are fast PCs with multiple core processors; high-end graphics cards (such as those that gamers use); big storage systems (often underestimated in costs); software for image processing, 3D manipulation and visualization, programming, and statistics; and staff to handle all these components. The team would ideally combine people with training in biology, anatomy, mathematics, statistics, programming, physics, and radiology. Devices for data acquisition do not have to be in the same lab or university, but they should be accessible conveniently, as via collaborations.

Virtual anthropology can be divided, with overlaps of course, into six operational areas (Fig. 1):

1. Digitize – mapping the physical world
2. Expose – looking inside
3. Compare – using numbers

4. Reconstruct – dealing with missing data
5. Materialize – back to the real world
6. Share – collaboration at the speed of the internet

All six are described in detail in a comprehensive textbook of this discipline (Weber and Bookstein 2011a). A summary of each of the six areas will be given below.

Digitize

The conversion of the real objects into virtual ones is obviously the first step in VA. There is a variety of technologies available today, some still sophisticated and costly, others simple in use and cheap. Digital data is a projection of continuous data into the space of integers. The range of numbers used for quantification is therefore limited to a discrete set of values, and the number of elements recorded is limited by the resolution of the sensor. Hence, the first two questions to answer are as follows: (1) Is it enough for the intended purpose (e.g., classification, hypothesis testing, modeling) to capture the surface of the object or is the whole volume of the object needed? (2) Independent of the first question, which resolution is reasonable? In paleoanthropology, many preserved features such as bone and enamel thickness, the cranial sinuses, the enamel-dentin junction of teeth, or the trabecular structures of the pelvis and long bones may carry important information with regard to interpretation of functional morphology and taxonomical assessment. Volume data, i.e., 3D data throughout the whole structure such as CT, is therefore often mandatory. In archaeology or face recognition of living subjects, for instance, surface data would satisfy many applications because the inner composition might be known, as, e.g., with stone tools, or not be part of the investigation. Surface scans can thus be ideal for the sake of saving time and money. Though many, if not most, paleo-questions would involve the inner structures of fossils earlier or later, surface scans can nevertheless be the choice of digitalization because volume data acquisition could simply be not possible for the moment, for instance, in the field or because no permission to transport fossils to the next volume scanner is available.

To scan the whole volume, all kinds of “tomographic” procedures (imaging by sections) are in principle applicable. Computed tomography (CT), a standard medical imaging procedure commonly used for scanning living patients; micro-computed tomography (μ-CT), an industrial imaging routine to examine materials in very high resolution; or magnetic resonance tomography (MRT), another medical routine to image patients avoiding ionizing radiation, are popular examples. The latter can capture soft tissues very well but hardly delivers usable signals from hard tissues such as bones and teeth. It is used to examine the brain, the heart, the cartilage in joints, and the like in living subjects. Its use for paleoanthropology is limited to very specific problems, predominantly to scan extant primates for comparative purposes (e.g., the relative size of frontal lobes (Semendeferi et al. 1997) or cranial base flexion during ontogeny (Jeffery and Spoor 2002)). In contrast, CT and μ-CT can cope easily with dense and very dense objects like bones, teeth, ivory, antler, shells, and stones. Like any of these tomographic methods, it delivers a stack of 2D images (called “slices”) that are combined to a 3D volume. Images are based on X-ray technology which means that radiation is emitted by a tube, the rays are partly absorbed by the object which is penetrated, and the remaining X-rays are recorded at a detector behind the object. In medical scanners, the object rests at a moving table and the tube-detector system rotates around it. In μ-CT, the object rotates instead which implies the necessity of a rigid fixation at the rotation table to avoid motion artifacts. Since paleoanthropology deals with dead material, the radiation dose is of low interest in both modalities (there might, however, be effects on color and preserved DNA; Paredes et al. 2012; Richards et al. 2012).

Each slice of the volume data consists of small picture elements, like those of any electronic image. While these elements in a 2D photo are called “pixels,” we call elements of 3D volume data “voxels” because they offer a third dimension, a thickness. Voxels carry information about their individual position in the x, y, and z grid of the volume – plus a specific value for their grey value. The inner composition of a scanned object is detected based on the different densities of materials which lead to different grey values of the voxels (a function of the attenuation of the X-rays). If that inner composition is to be expected homogenous, then there is no argument of using a tomographic technology. If, in contrast, different materials or change of material over space can be expected, then it is the appropriate procedure. CT can deliver a resolution of roughly a millimeter down to ~200 μm. Features being smaller cannot be acquired. μ-CT starts somewhere around 100 μm and can go down to 1 μm, depending on the capabilities of the system (e.g., the diameter of the micro-focused X-ray beam, the size of the detector elements) and the applied magnification which again depends on the size of the object and the scanner geometry. Many recording chambers of μ-CTs are limited to relatively small objects (usually only some centimeters in diameter). Only a few machines can handle large objects of the size of a human skull or femur (e.g., VISCOM X8060 II, see www.micro-ct.at). A further increase in contrast quality and resolution is possible with synchrotron tomography which may go down as far as 0.7 μm (Sanchez et al. 2012). However, research times at those facilities are quite in demand and therefore hard to obtain.

The resolution of the data should be generally “good enough for the purpose” (Weber and Bookstein 2011a). While it rarely makes sense for the investigation of the gross geometry of a skull to go down with resolution lower than 200 μm, another scan at 50 μm could still be too coarse for the analysis of tooth wear facets. A good question to start is thus: What is the smallest structure that needs to be detected? And why not digitize everything using μ-CT? Firstly, the accessibility to these machines is still very restricted. They are immobile or, at best, can be transported only with great difficulty. Secondly, mammoth data volumes emerge (e.g., a cranium with 50 μm voxels is roughly 70 GB data), which require high-end computers for their processing. This is where the technical development of computers and storage media still lags, in an affordable price range, behind the possibilities of the technical scan. Thirdly, only small objects can be examined, while crania, jaws, or long bone fragments in many cases do not fit into the recording chamber, with exceptions as mentioned above. For precious objects such as fossils which can undergo an examination perhaps only once, μ-CT is definitely the preferred choice because it delivers data good enough for virtually all purposes and for the middle-term future (even if we have to await technical development to fully use it).

Surface scanning on the other hand does not allow looking even a nanometer below the exterior interface, but, depending on the system used, can digitize the surface in very high resolution too (also in the μm range). Scanners are often based on laser beams or structured light (dark and bright stripes) that are projected over the object. A sensor is measuring the reflected light, respectively the pattern of stripe distortion. Since the geometry of the light/pattern emitting and receiving system is known, the object geometry can be computed by means of triangulation. The acquisition of one such "shot" can be very fast (within seconds). But comparable to photography, it represents only one view. Hence, the object has to be rotated and captured again and again, with overlapping areas. Smart routines in the software will stitch together the different views until the whole object surface is recorded in all dimensions. Data sets are rather small compared to volume data (because the objects are "hollow"), and in some cases also texture/color information can be recorded. This can be an important additional aspect in paleoanthropology – to keep this kind of information in the analysis (which is not possible with any of the tomographic procedures). Surface scanners are easier to transport than CT or μ-CT scanners and a magnitude cheaper. Applications in the field are thus feasible (if there is electric power available). Stereoscopic photography is also an alternative to obtain 3D data from multiple images taken from different views. Recent software packages (e.g., PhotoModeler® http://www.photomodeler.com) assist in calibrating the camera system and identifying overlapping points on images to create a 3D model of the object (Paul et al. 2013).

For scanning bones and fossils, there shaped up a list of do's and don'ts in practice. For instance, all metal parts (e.g., fixing pins, clips) should be removed from the object to avoid artifacts, the gantry tilt in medical devices should be kept at zero, an appropriate *field of view* to maximize resolution and the smallest possible slice thickness to minimize the *partial volume effect* should be chosen, the contrast should be maximized and CT scale overflow artifacts avoided, and the kernel (the convolution filter used for back projection) should be neutral to slightly hard. In any case, the raw data should be kept. New reconstructions can be computed afterward from this source. And after scanning, it is a matter of courtesy to share the data and leave a copy with the institution that hosts the collection of fossils. The brevity of this article does not allow for a discussion in length, but for more technical advice, see, e.g., Spoor et al. (2000); Zollikofer and Ponce de León (2005), or Weber and Bookstein (2011a).

Expose

There is nothing to expose with surface data, as mentioned above, because only the visible surface was recorded. Working with tomographic data, the outer *and* the inner structure can be examined. In contrast to invasive techniques such as histological thin sections or grinding, the advantage is that the object does not have to be destroyed and only has to be touched for transport to a scanner and back. Its interior can be inspected by browsing through the stack of images (like most radiologists still do with their light box examining CT or MRT scans of patients) or by *segmenting* structures of interest as 3D objects. Segmentation means to separate particular areas of the image from their neighborhood and address them as different logical entities. For instance, the brain in a MRT scan is often segmented from the surrounding liquor, meninges, bones, and muscles to work on its morphology. Paleoanthropologists do the same with the interior of the braincase, the only remainder in fossils to infer speculations about our ancestor's cognitive capacities. In a dried skull, and often in fossils, the braincase is filled with air which has a different grey value (black) than the bone (white). There are semiautomated algorithms (mostly thresholded region growing) available in many programs (e.g., Amira™, Analyze™) that help labeling the borders between the regions without much manual intervention. The latter is important to approximate the goal of reproducibility, thus avoiding subjective influences. Once this is done for each slice of the volume, there is a new object that is called "virtual endocast" (Weber et al. 1998). It can be rendered on a computer screen (Fig. 2), where it appears as a "positive" of the formerly hollow cavity. Surface details like imprints of brain convolutions or vessels can be described, and it can be measured, e.g., the cranial capacity (volume). Likewise, other hollow structures can be created as virtual endocasts, for instance, the frontal and the maxillary sinuses or the pulp of a tooth.

Since the brain development is one of the critical issues in human evolution, endocranial endocasts are important sources to compute indices such as the encephalization quotient, which is based on the estimated brain to body size ratio (Martin 1983). Cranial capacity, i.e., the volume of the endocranial cavity, is, however, not equal to the size of the brain but about 10 % less (Holloway et al. 2004). Virtual endocasts were used in many fossil studies to infer an approximate brain volume or other descriptions (Conroy et al. 1998, 2000; Recheis et al. 1999; Falk et al. 2000; Tobias 2001; Prossinger et al. 2003; Bräuer et al. 2004; Carlson et al. 2011; Curnoe et al. 2012) and were also used for modern humans, primates, and vertebrates (Colbert et al. 2005; Rowe et al. 2005; Macrini et al. 2007). Unfortunately, they provide no direct information with regard to the internal structures of the brain, e.g., the number of neurons and their density and histological structure, or about the connectivity between areas of the brain. But beside the mere volume, the full range of the morphometric tool kit (including landmarks, curves, and surfaces, see below) can be used for the quantitative comparison of the internal morphology just as for the outside of skulls. Beside size change, it is mainly changes in the overall proportions of the brain or the

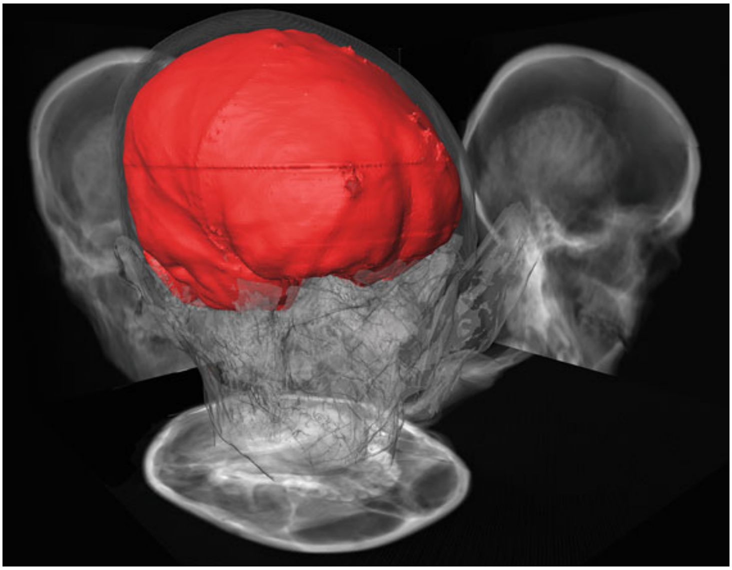


Fig. 2 Virtual endocast of the Tyrolean Iceman "Ötzi" which represents the size and shape of the endocranial cavity. The projected X-rays in the background show the actual shrunken brain

proportions of its components such as the size of the frontal cortex and cerebellum (Seidler et al. 1997), or the parietal lobes (Bruner et al. 2003), or the pattern of vascular supply (Neubauer et al. 2004) that inform about hominin evolution. Also the ontogenetic patterns of brain development changed in the course of evolution, which can be studied in fossils and in comparison to extant apes (Neubauer and Hublin 2012).

Staying with the brain for a moment longer, there are of course applications of the VA action "expose" to extant humans as well, reaching far into medicine. The fetal alcohol syndrome, for instance, leaves its traces in the connecting structure between the hemispheres, the corpus callosum. With the use of MRT scans and semilandmarks along its midline, researchers (Bookstein et al. 2006) could clearly show a specific geometric signal indicating brain damage in this class of birth defect that is triggered by alcohol abuse during pregnancy. The method is even used in American courtrooms to detect this damage in the brains of certain convicted murders at risk of a death sentence. Virtual endocasts of recent humans have also been used to illustrate the effects of a new surgical intervention to relief intracranial pressure in cases of severe brain edema. "Posterior-hinged circular craniotomy" (Traxler et al. 2002) is applied when conventional therapy and trepanation fails. The whole calotte is cut, with the only exception of a small region at the occiput to protect the vital blood drainage via the sagittal sinus. But the gain in volume at a certain degree of frontal elevation of the calotte is almost impossible to measure on a patient while it is quite simple by means of virtual endocasts where this elevation can be simulated on the computer and volume increase be measured and correlated with skull shape and other factors such as sex.

Coming back to paleoanthropology, “electronic preparation” of specimens is another important domain of VA. A form of interest in many fossils is not or only partly accessible because it is covered by some foreign material, sometimes called “matrix” or “encrustation.” The foreign material must be removed without jeopardizing the surface of the object any more than necessary. Physical preparation is a manual procedure that requires highly trained and experienced staff with good eyesight and steady hands. Miniature chisels, air hammers, sandblasters, and the like are used to remove the matrix bit by bit. Nevertheless, there is a considerable element of risk because the matrix could be excised too deeply, destroying actual fossil bone. Good preparators avoid such errors by working very slowly. Still, internal features like sinuses or cranial cavities are impossible to uncover.

Electronic preparation, in contrast, is based on volume data (surface data do not inform about internal characteristics) which allows access at any point of the object. For fossils, these are typically CT or μ-CT scans. If the fossilized bone displays a distinctly different range of grey values (density) than the matrix does, the removal of the foreign material is a fairly straightforward job. The material properties of matrix vary, however, widely, as do the difficulties associated with their virtual removal. But one overwhelming advantage of computer-based methods is immediately evident: the original specimen is not impaired. There is no “undo” command for operations on physical objects.

In difficult cases, there is overlap in grey values (density) between fossilized bone and matrix or the matrix is heterogeneous, as when gravels and grains of rock are embedded in calcareous sand. Sophisticated filtering might be necessary during segmentation to find a clear boundary between bone and matrix. Such filters to enhance the boundaries may involve a single application of a Sobel, Laplace, Low Pass or other filter (Weber and Bookstein 2011a), or even a fine-tuned sequence of many filters (e.g., Prossinger et al. 2003). Morphological filtering is another routine to support the separation of logically different units by breaking up tiny bridges that may be left over after region-growing procedures or to smooth the results. There is a huge literature out there about digital image processing, which is not related to VA specific tasks, but very helpful to consult (e.g., Gonzalez and Woods 2008; O’Gorman et al. 2008; Yoo 2004).

Compare

Morphological studies involve the need to capture the shape and form of objects and to compare individuals or samples to each other. Typical questions that arise are the following: How does the average form look like? How does form vary in a population around this average? How are two groups differing from each other? What might be the functional meaning of such form differences? In VA, the aim is to treat the shape and form of specimens or groups by means of numbers, which ideally consider the whole form under investigation rather than “atomizing” it by describing countless separate traits (e.g., occipital bun, high parietal boss, low cranium, projecting midface) by words or by characterizing form by a restricted and unrelated set of measurements. This brings along some advantages. The numbers help limiting subjectivity as far as possible. Considering the whole form at once avoids treating the skull as a set of features that could not actually be independent. And using computing power and memory facilitates the comparison of hundreds of "traits" (actually then the whole form at once) from hundreds of individuals simultaneously (see, e.g., Gunz et al. 2009a). The human mind is not able to keep an overview over such large data sets and tends to overlook facts and introduce its opinions. Paleoanthropology is probably not a bad example for this inherent imperfection of the human analogous computing mode (which has admittedly great advantages otherwise, see below).

VA uses machines to do the computing of powerful statistics, not to interpret them meaningfully. This is still the domain of the researcher in front of the machine (with his/her integrative brain, a feature that machines are still very bad in simulating). Nevertheless, this way offers a step toward more reproducible results, a fundamental claim of any natural science. There are several different techniques to quantify shape and form, for instance, outline approaches such as elliptic Fourier analysis (EFA, Kuhl and Giardina 1982) capturing closed contours quite well and not being dependent of evenly spaced points or equal number of points across specimens, or Euclidean distance matrix analysis (EDMA, Lele and Richtsmeier 1991) based on distances between landmarks and thus well suitable for sufficiently large sets of caliper measurements. Another approach is called "geometric morphometrics (GM)" which uses multivariate statistics based on 3D coordinate data. Avoiding distances and angles (which have some specific disadvantageous statistical properties such as introducing artifactual covariance structures (Rohlf 1999) and biased mean estimates (Rohlf 2003; Slice 2005)) and orientation problems, GM retains all geometric information contained within the data. A combination of outline and landmark-based approaches would be desirable in some cases (Baylac and Friess 2005). There are of course many pros and cons for the individual approaches. The space of this review article does by far not allow for a detailed discussion; however, some references are suggested to form an opinion (e.g., Bookstein 1991; Rohlf and Marcus 1993; Bookstein 1996; Dryden and Mardia 1998; Lele and Richtsmeier 2001; Slice 2005; Weber and Bookstein 2011a).

Comparisons of biological forms have to be kept under the control of biological theory: the rule of homology (comparing like to like). GM utilizes a particular formal technique, that of landmark/semilandmark points, which enforces this rule. Landmarks are specific points on a form or image of a form located according to some rule. There are several types of landmarks corresponding to the method how they are identified. For instance, they can be located at the crossing of bony sutures or at extreme points of curvature or along ridges (see landmark types I–VI in Weber and Bookstein 2011a). Central to the GM approach are some key elements such as generalized procrustes analysis (GPA; Gower 1975; Marcus et al. 1996), principal component analysis (PCA), and thin plate spline warping (TPS; Bookstein 1978, 1991) that lead to representations of form by size along with shape coordinates and

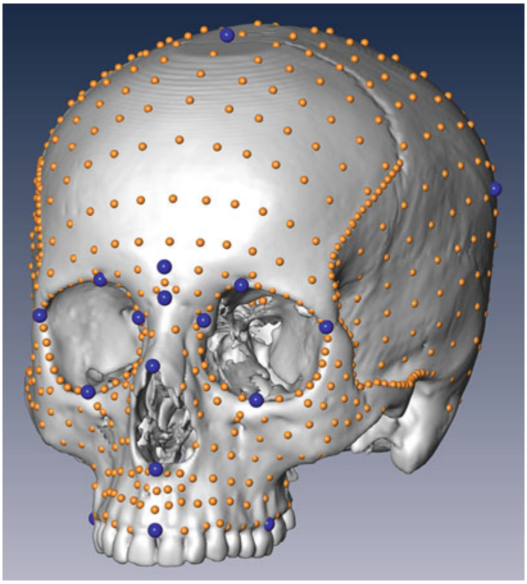


Fig. 3 Rendered 3D model of human cranium with 25 classical landmarks (biologically homologous measuring points) as dark spheres and 824 semilandmarks (geometrically homologous measuring points) as bright spheres. Almost the complete geometry of the cranium can be captured with this method

visualization not only of single forms but also of comparisons via the deformation grids that illustrate and formalize shape differences between geometrical objects. Moreover, the way data are represented allows the scientist to compute means and variances of groups at the same time that differences between two specimens or mean configurations are visualized as deformation grids. Importantly, size can be kept in or otherwise be eliminated from the analysis (the message to remember is *form is shape and size*).

Classic landmarks have a long tradition in anthropology (for a comprehensive list see, e.g., Martin 1914), but they are rare on many structures, for instance, on the braincase, where obviously whole regions on the frontal, parietal, occipital, and temporal bone offer no landmarks. The same problem applies to many other structures, also in the viscerocranium, on most of the postcranial skeleton, on the teeth, and of course on the face and body of living humans. The GM machinery allows identifying the so-called semilandmarks on curves and surfaces. These points are geometrically homologous (Bookstein 1989; Gunz et al. 2005) and can capture previously unattended regions. The 3D model of the human cranium provided here (Fig. 3) shows 25 classic landmarks like those that are usually applied to “caliper” studies and 824 semilandmarks on curves (temporal line, zygomatic arch, orbita, alveolar rim of the maxilla) and surfaces that capture previously unattended regions. The semilandmark approach obviously considers more information and thus can support more sophisticated statements about shape and form differences between groups or individuals. However, these semilandmarks cannot be identified in the physical world, rather they have to be constructed following certain principals that can only be followed in the virtual world. In practice, semilandmarks (sLM) are identified on one template specimen (any from the sample to start with) and then projected to the other specimens in the sample. After this step, they need to be "slid" (curve sLM have 1° of freedom, surface sLM have 2° of freedom, free points have 3° of freedom). Semilandmarks are matched between specimens under control of some global energy term, such as the bending energy of the thin plate spline. After this first round, the template specimen is replaced by the new Procrustes average configuration, and the process repeated until no changes appear. The number of semilandmarks needs to be sufficient to capture the spatial nature of variation or covariation that will emerge from multivariate analysis of these shape coordinates (Weber and Bookstein 2011a).

What works well with skulls and bones also works with stones and artifacts, soft tissues, or even cars. Particularly, the last years have seen the applications of geometric morphometrics in the context of quantitative analysis of lithic assemblages, for instance, using landmark/semilandmark approaches (Lycett et al. 2010; Archer and Braun 2010; Buchanan and Collard 2010) or surface areas (Lin et al. 2010). GM is widely used to characterize facial shape and its asymmetries and relations to other tissues (e.g., Fink et al. 2005; Bugaighis et al. 2010; Pflüger et al. 2012; Meindl et al. 2012; Kustár et al. 2013), and even the shape of "car faces" was associated with trait attribution (Windhager et al. 2012).

The common problem of all these applications of GM is that they need a fairly rich theoretical background before they can be used properly and that programming knowledge is often necessary to translate theory into results. In the early 2000s, mathematical packages such as Mathematica™ (Wolfram Research) or Matlab™ (MathWorks) had to be used to write routines that perform generalized procrustes analysis or thin plate spline warping. Not every good biologist is necessarily a good programmer, thus the application of GM often stranded for practical reasons. While the *development* of new algorithms inevitably needs the interdisciplinary action (a core domain of VA) between biologists, mathematicians/statisticians, and software engineers, the *application* of established procedures became meanwhile easier with some software solutions that did not reach the standard of commercial products but are "usable for the accustomed user." Morphologika (https://sites.google.com/site/hymsfme/downloadmorphologica) was one of the first such solutions that could process 2D and 3D data and handle GPA, PCA, regression, and warping. Morpheus (http://www.morphometrics.org/) by Dennis Slice, Viewbox (http://www.dhal.com/viewboxindex.htm) by Demetrios Halazonetis, the suite of tps programs (http://life.bio.sunysb.edu/ee/rohlf/software.html) by James Rohlf, and edgewarp (http://brainmap.stat.washington.edu/edgewarp/, restricted to Linux) by Bill Green offer access to some or almost all GM routines to a varying degree. In an attempt to spread knowledge among young European scientists and to establish VA-related infrastructure, the EU-funded project EVAN (European Virtual Anthropology Network) has developed and released the EVAN Toolbox (ET; http://www.evan-society.org/node/23, Fig. 4). Beside for research purposes, ET has turned out to be a fairly good teaching tool so that the issues of GPA, PCA, TPS, group mean comparisons, regression, reflected relabeling, or the analysis of asymmetry (Mardia et al. 2000) lose some of their frightening flavor during practical application with real data. Programming is not necessary because all operations can

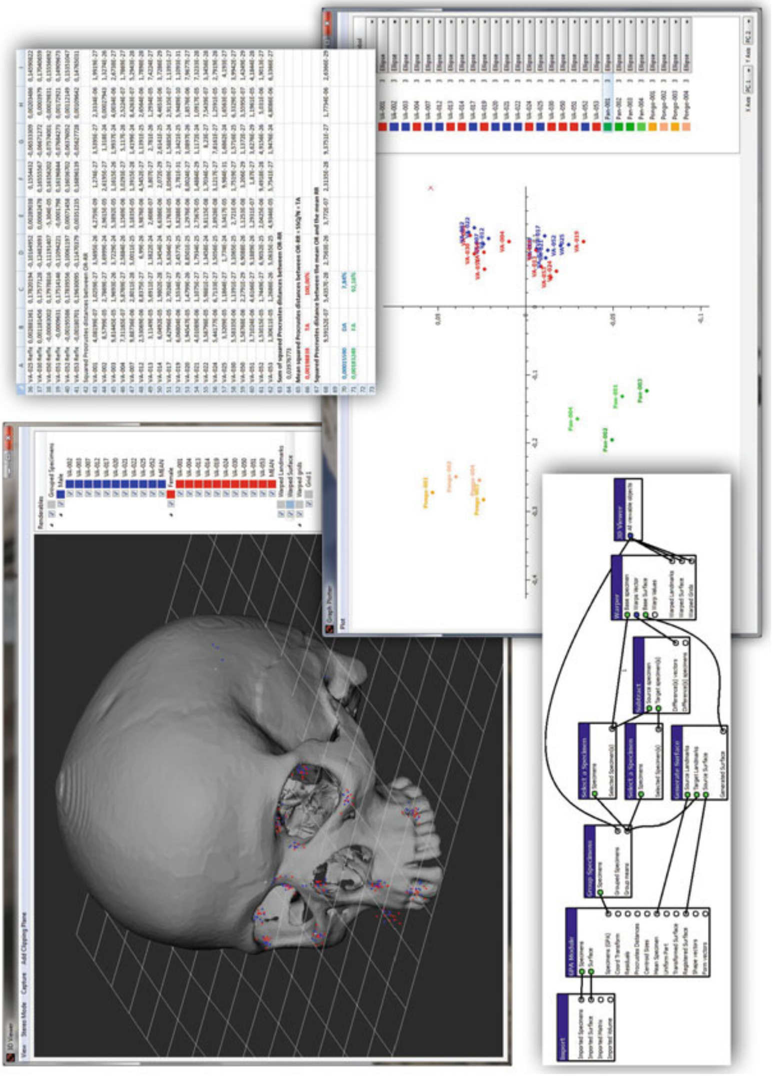


Fig. 4 Screenshots of the EVAN Toolbox. Mean shapes can be warped between sexes (*top left*); Procrustes distances are exported into a spreadsheet for further computation (*top right*); principal component analysis of shape for modern humans, chimps, and orangutans is shown for the first two relative warps (*bottom right*); a typical visual programming network to operate analyses (*bottom left*)

be put together in visual programming networks, just as modules that are connected by lines.

Independent of which software and methodological approach is used, it seems most important for advances in quantitative morphology to train young people on a broad scale to use these techniques of the twenty-first century.

Reconstruct

Reconstruction in virtual anthropology refers to the form and shape of biological objects, while in archaeology it refers to the form and shape of artifacts or buildings. Whenever the present form of an object fails to correspond with its supposed original form, reconstruction might be needed. Taphonomic processes, but also damage during excavation or manipulation, can lead to four principal kinds of disturbances of a form (Weber and Bookstein 2011a). All of these apply similarly to archaeological objects:

1. An object can be broken, but (almost) all pieces are preserved. This is called a *type 1* disturbance, e.g., a broken cranium, even if it consists of many pieces, which can be fully restored using glue.
2. Whenever parts of an objects are missing, it is called a *type 2* disturbance, e.g., a humerus that is basically intact but missing its head.
3. An object can be deformed. That is a *type 3* disturbance, e.g., a fossilized pelvis that shows plastic deformations due to million-year-long pressure of the overlaying rocks.
4. An object can be intact but not be directly accessible because it is covered by a foreign material. This *type 4* disturbance was mentioned above in the context of electronic preparation, e.g., a finger bone that is embedded in calcareous sands.

Of course, all kinds of combinations of these disturbances may exist, and in fact, we rarely find one alone (e.g., there is often broken & missing, broken & covered, missing & deformed & covered, etc.). We speak of reconstruction when a disturbance has been recognized and corrected (Weber and Bookstein 2011a). The types of disturbances introduced above help thinking about the varieties of reconstruction problems that one will face during the process. Single types 1 and 4 problems can have unique solutions, at least in principle (there are only very limited degrees of freedom to put together a complete 3D puzzle, and e-preparation can eliminate matrix in many cases entirely). For most type 2 problems, there is no unique solution, and the same is true for type 3 problems (except for those where the deformation forces are known or one half of a symmetric structure is unaffected and can be mirrored). This is because the form of missing or deformed parts has to be estimated which involves data about undisturbed forms of the same group of objects and assumptions.

A reconstruction can therefore never duplicate the original. It can approximate it. The role of VA in reconstruction is to make the various manipulations reproducible, ergo to involve numbers in the process as far as possible. Biological forms follow constraints, for instance, laws of physics such as gravity, material strength, and load; they respond to the mechanisms of evolution such as the selection of environmentally favorable traits, and anatomical modules develop in concert (integration). The numerous genetic, developmental, and functional factors applying to the form of biological objects enable us to reduce the "degrees of freedom," the uncertainties, for a reconstruction. However, there is also a lot of interindividual variation in a group, another principle of evolution. For instance, the form of an upper jaw (maxilla) is of course known in principle for modern humans, but each human has a slightly different form which is determined by genetic and environmental factors. Bone remodeling happens during the whole life. A maxilla's form is depending on the inherited skull form, the individual loadings (related to muscles and diet), the preservation and position of teeth (e.g., some might be lost, some inclined forward or backward), or other behavioral aspects (e.g., teeth might be used as tool or clenched during the night). In biology, we can thus reconstruct most parts only based on a reference data set (a sample of similar organisms) and with a particular likelihood. In contrast, if a portion of a ceramic vase is missing, it could be relatively easy to recreate its initial form because it would follow a pretty strict rule of a smooth surface (especially if done with a potter's wheel). With fossils, it becomes actually more difficult because the reference sample might be small or even absent. In those cases, reconstruction resorts to the closest sample available – a compromise.

The advantage of using VA in reconstruction is that reference data and assumptions have to be made explicit. There is no mumbo jumbo of the expert who pulls out a reconstruction of the hat like a rabbit. Everything is based on measurements and explicit statements can be made, e.g., which kind of reference data was used or which geometric constraint (e.g., bilateral symmetry) was applied. In lucky cases, the task may boil down to limit the 6° of freedom (three to translate, three to rotate) to possibly zero when putting pieces together or to apply a priori knowledge about the form (e.g., smoothness of curvature, radial or bilateral symmetry) during estimation of missing parts.

In opposite to a physical reconstruction, a virtual one is not depending on sources of irritation such as gravity, glue, or having only one trial. This is one of the reasons why they appeared already very early in the history of VA (Kalvin et al. 1995; Zollikofer et al. 1995; Thompson and Illerhaus 1998). Absolute control over fragment translations and rotations can be achieved with many software packages, particularly in the CAD (computer aided design) domain, that also support the process with aiding constructions such as B-splines or NURBS (non-uniform rational B-splines). Aside from a highly controlled merging of pieces on the screen (already an important improvement) and including occasionally mirroring of pieces, as we see it frequently in *anatomical* reconstructions (Zollikofer et al. 2005; Ryan et al. 2008), some other technology introduced under "compare" can be used for estimating missing or deformed parts (i.e., types 2 and 3 problems).

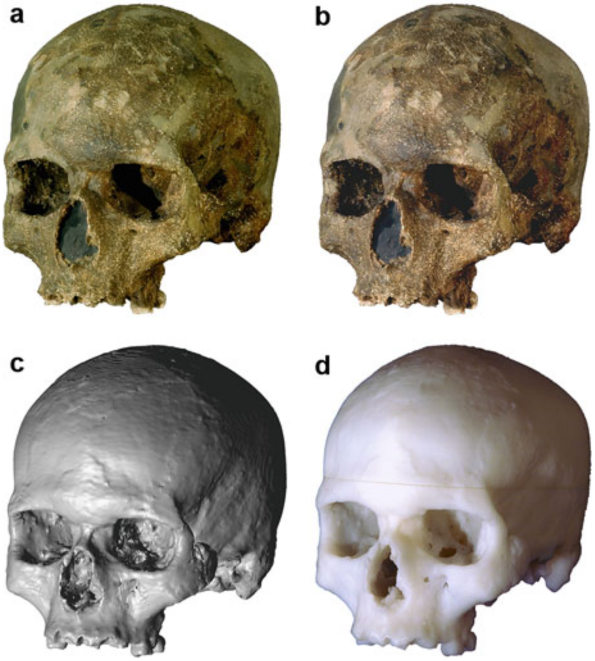
Thin plate spline interpolation (Neubauer et al. 2004; Gunz et al. 2009b; Grine et al. 2010; Weber and Bookstein 2011a; Senck et al. 2013) can be applied for *geometric* reconstruction. It uses a map of landmarks and semilandmarks from a complete specimen (the “reference”) and whatever is left on the specimen to be reconstructed (the “target”). It is a deformation of the reference that is computed to match the location of the corresponding points on the target while filling in the rest of the information. Noteworthy, this is not a simple “copy and paste” action, rather it takes the preserved morphology of the target into account and adapts the missing parts, which are filled in from the template. Applications range from fossil reconstructions (Gunz et al. 2009b; Benazzi et al. 2011a, 2013a) to the preoperative implant planning for large skull defects (Heuzé et al. 2008). There is, however, a caveat of TPS-based reconstruction: it should not be used when it is an extrapolation – when the region being reconstructed extends substantially beyond the limits of the region present in the target (i.e., do not reconstruct the face if just the braincase is preserved). Nevertheless, it works particularly well to reconstruct smooth surfaces, such as the neurocranium, when coordinate-based landmarks and semilandmarks are sampled densely. Alternatively, a reference database can be used to drive reconstructions via multivariate regressions, which rely on the covariation among the observable coordinates (Gunz et al. 2009b; cf. Neeser et al. 2009). However, the sample has to be sufficiently large to increase the certainty of estimates – a demand that is rarely met in paleoanthropology. TPS in contrast just needs one reference specimen but the result is entirely depending on it. Whenever more than one reference specimen is available, multiple reconstructions can be computed to assess their range of possible variation (Gunz et al. 2009b; Benazzi et al. 2011a; Weber and Bookstein 2011a) or the sample average can be computed and used for the TPS warping (Senck et al. 2013).

In a science that is highly depending on reconstructed forms on the one hand (be it for morphological comparison or just for museum display) but which has only a few intact templates to offer on the other, we naturally have to make compromises. In some cases, even a composite fossil (Kalvin et al. 1995) might be a solution to make a further step in a heuristic process. Strait et al. (2009), for instance, have used a fairly complete but edentulous cranium of *Australopithecus africanus* (Sts 5) and a fairly complete dentition of another member of this taxon (Sts 52) to be able to simulate loadings on the cranium during different modes of bite. Though both specimens were in a similar dental stage and the preserved tooth roots of Sts 5 were matched with the teeth of Sts 52, the reconstruction would certainly deviate within limits from the original appearance of Sts 5 in its lifetime. However, these deviations could be regarded small enough to be accepted in a situation where a more persuasive solution is impossible (at least until a complete and undeformed cranium with dentition is unearthed and accessible).

Materialize

There are *two* sources for appraising morphology in classical anthropology, original specimens and their casts, and there are *two* in virtual anthropology, digital copies on the screen and rapid prototyping models deriving from these copies (Fig. 5).

Fig. 5 The Upper Paleolithic cranium of Mladeč 1 as (**a**) original, (**b**) traditional cast, (**c**) virtual specimen on the computer screen, and (**d**) rapid prototyping model (With permission of the Natural History Museum Vienna)



For teaching and training purposes, as well as for permanent museum display, real models can be more desirable media to create knowledge than virtual ones. In any case they are essential when there is no computer available. But also for the researcher, real models provide a substantial aid to understand three-dimensional relationships of spatially complex structures. Architects are certainly among the best trained people with regard to spatial imagination, but in practice many of them still build real models of constructions to appraise complex interactions of structures. There is a German word called "begreifen" which not by accident means both "to touch" and "to understand."

Rapid prototyping (RP) technology was realized in the 1980s to facilitate quick and relatively cheap manufacturing of industrial prototypes. The idea is to have something real in hand that was initially created in a computer environment, a newly designed telephone before mass production, an implant to train with before surgery, a downscaled model of an airplane to be tested in the wind tunnel, and the like. The principle behind all kinds of different RP techniques out there is to build an object layer by layer with small elements. This is actually a very ancient idea looking at the Great Pyramids of Giza that are constructed the same way, layers of stones over layers of stones. The great advantage of the relatively slow layer-wise approach is that even hollow spaces and undercuts can be built which is not possible with other techniques, e.g., with CNC (computer numerical control) machinery.

Stereolithography (STL) was one of the first and still is one of the most advanced procedures which allow producing accurate models down to a resolution of ~0.1 mm.

The STL data generated during preparation derive from 3D volume or surface data, e.g., CT or surface scans, or constructed surfaces like CAD objects, or a reconstructed fossil. They serve to control a mobile mirror that directs an ultraviolet (UV) laser beam in accordance with the layer geometry. Where the UV laser beam comes into contact with a photosensitive liquid acrylate or epoxide resin, it hardens. Then the part is lowered deeper – by the thickness of one layer – into the liquid polymer bath. The surface must be leveled initially by a recoating system and then the next layer is hardened. This process continues automatically until the production of the 3D part has been completed. Supporting constructions permit the fabrication of "overhanging" parts that would otherwise float away before they are connected to the structures above.

Other methods use powders rather than liquids (e.g., Z-printing, laser sintering) or meltable plastics (e.g., fused deposition modeling) applied through heating nozzles, comparable to what a printer does with ink. There can be huge differences in the price, the speed, and in the quality of models (see Weber and Bookstein 2011a for an overview). A decision with regard to the planned application is thus needed – cheap, accurate, enduring, fast, transparent, and multicolor are some of the options to be considered.

Whatever the choice of method is, any type of RP model has some advantages over casts in the following respects:

1. There is no mold that is aging (of course the model itself will age, but it can be reproduced to 100 %), only the digital data has to be kept save.
2. There is no contact to the original object, only contactless scanning is required, a big issue in many cases of fragile and brittle specimens with porous surfaces.
3. Most biological objects feature hollow structures and undercuts which are no problem to be realized with RP. To access them, models can be built as separate parts, e.g., a skull with removable calotte to enable inspection of the cranial cavity.
4. Models can be up- or downscaled (e.g., 25 %-sized "pocket replicas" of skulls or a 400 %-sized model of trabeculi in a cut of the femoral neck).

Of course, there are drawbacks of RP procedures as well: Some of them are rather expensive (a stereolithography of a skull can cost more than € 1,000). However, there is a growing market of desktop 3D printers that permit production of models in a very low price range (some machines are cheaper than a STL model). The other important drawback is the limited resolution of RP models, somewhere in the 100 μm range. It depends on the incoming data, which in the case of medical CT is even lower (typically 200–500 μm), and the characteristics of the RP procedure itself. On account of their layered structure, the aliasing effect (jagged surface) of all RP models can be recognized – a smooth surface can be achieved only by intensive reworking. Recent developments can improve resolution considerably by a combination of micro-computed tomography and micro-stereolithography. The size of objects is limited, but a layer thickness of less than 25 μm is possible. A first application to a fossil object (lower molar of an *Australopithecus afarensis*) is described in Weber and Bookstein (2011a, p. 321).

The usefulness of rapid prototyping models has been amply argued over the years. The first stereolithographic model in anthropology was by the way done on the Tyrolean Iceman "Ötzi" to get access to the skull of the precious mummy (Seidler et al. 1992; zur Nedden et al. 1994). The full potential for anthropological application turned out soon thereafter (e.g., Hjalgrim et al. 1995; Zollikofer et al. 1995; Seidler et al. 1997; Recheis et al. 1999; Ponce de León and Zollikofer 1999; Weber et al. 2001; Kimbel et al. 2004). In the medical field, RP models are used as well since the early 1990s, particularly for implant planning (e.g., Klein et al. 1992; Anderl et al. 1994; Yau et al. 1995). There is thus a considerable overlap in techniques used in paleoanthropology and surgery planning, which opens possibilities for collaborations and jobs for (paleo)anthropologists.

Share

Speaking of collaboration, most contemporaries have recognized that scientific progress can be advanced by sharing methods and data resources. Studying biological and evolutionary questions, it is of the essence to talk about intragroup and between-group variation. There is one very simple guideline coming from statistics: The larger the samples are the sharper is our picture with regard to variation and differences. With the introduction of the Internet, some sciences saw a progressively increasing behavior of sharing information. Open access journals are meanwhile widespread, and data archives were and are created in any field of research. Probably the most consequent application is found in genetics, where the human sequences and meta-information are published as a matter of course (e.g., http://www.ncbi.nlm.nih.gov/gene, http://www.genecards.org/). Paleoanthropology, however, is a field where the idea of sharing data for the sake of creating knowledge is still not pervasively accepted. The first electronic archive of hominin fossils was created in 1999 (http://www.virtual-anthropology.com/3d_data/3d-archive), and the idea of an opening – "glasnost in paleoanthropology" – was expressed soon after the Millennium (Weber 2001). The paleo community saw reviews and conferences on the topic (Gibbons 2002; Soares 2003; Delson et al. 2007; Kullmer 2008; Mafart 2008), and some further archives were established (e.g., NESPOS, EVAN-Society, ORSA, DigiMorph, Paleoanthportal, RHOI, AHOB, Visible Human Server). However, researchers and curators remained reluctant (Weber and Bookstein 2011b). The digital@rchive of fossil hominoids is still the largest database providing access to a significant number of very important hominin fossils without restrictions.

Beyond doubt, there are a lot of difficult questions involved in this problem, for instance, how to protect the legitimate interests of the discoverers who often invested considerable amounts of time and money, in some cases even risking their life in the field, to make their findings. How should large funding agencies and journals act to enforce publication of data, rules that are somewhere hidden in the fine print? It seems reasonable to allocate sufficient time for the discoverers to work on their specimens. Yet, there are large numbers of fossils that are not accessible, even decades after their discovery. As mentioned at the beginning, it is a quite essential claim in science that results can be checked by others, particularly if a new taxon is described and established. As a consequence, there is thus a reasonable demand that at least electronic data from specimens should be accessible after a publication, or, if nothing is published, after a certain number of years.

Gene sequences of humans are accessible because they represent our common evolutionary heritage and an important resource to gain further knowledge for the benefit of all. When a fossil is discovered, it is usually owned by the country from which it originates. The fossil is then carefully stored in a national institution such as a natural history museum and administered by the local curator who acts as the representative of the owner (which is the country but not the curator). Although it is alright that the country has this exclusive control over its property, there is another obligation associated with the curation – to grant access to all researchers who have a reasonable research question and the capacity to answer it. A hominin fossil contains data about our common evolutionary heritage, as well as genes do. Restriction of access to data cannot be found on the list of privileges associated with ownership. In other words, fossils may be owned, but they may not be copyrighted.

Data itself can have diverse characteristics which are associated to the mode of measurement and to the user's context. It is necessary to reflect these qualities of data because they are relevant for access policies and structuring data archives. For instance, when a data archive is to be established for paleoanthropological purposes, a number of researchers will probably be interested in data from hominids, e.g., a CT scan of an *Australopithecus* skull or a chimpanzee thigh bone. These data can be called "source data" because they were mainly acquired by a machine (e.g., CT, μ-CT, surface scanner) and are thus much less biased by any intellectual treatment of colleagues than another kind of data that can be called "derived data." The latter would be, for instance, coordinate measurements of landmarks or a virtual reconstruction because these tasks involve an observer's perception and include individual interpretation. It is a fundamental issue for access rights on the one hand and for further application of data on the other to be aware of this history. An anthropologist will ultimately also want to make use of the geochronologists', paleontologists', or pathologists' data archives in order to acquire another sort of data, "contextual data" pertaining to the specimen under examination. Electronic archives have to be structured according to these needs.

In the first place, clear access policies are necessary; it is secondary what they actually are. A minimum standard could be that museums and other organizations accommodating valuable material in their collections make accessible list of specimens and statements as regards curation and access policies. A recently upcoming attitude of a "data embargo" continuing over many years after fossils have been scanned by some researchers should also be condemned because it does not lead to an opening and the protection of specimens but just to other data syndicates preventing access and to the desire for re-scanning.

Biomechanical Analysis of Biological Objects

The mechanics of organismal structures can be studied in various ways, including physical and mathematical models (Demes and Creel 1988; Spencer and Demes 1993), in vivo and in vitro experimentation (Hylander 1979; Ravosa et al. 2000; Daegling and Hotzman 2003; Wang and Dechow 2006), and, since the availability of adequate computer technology, computer-based simulations (Sellers and Crompton 2004; Koolstra and Van Eijden 2005; Rayfield 2005; Ross 2005; Dumont et al. 2009; Strait et al. 2009, 2010, 2013; Kupczik et al. 2009; Wroe et al. 2010; Benazzi et al. 2011b; Gröning et al. 2011; O'Higgins et al. 2012). One approach to study how mechanical systems such as the musculoskeletal apparatus move under the influence of forces is Multibody Dynamics Analysis (Curtis et al. 2008, 2013; Fitton et al. 2012; O'Higgins et al. 2012). Finite element analysis (FEA), another engineering technique, has been particularly widely applied in clinical and evolutionary biomechanics because it allows exploring how objects of complex geometries respond to external loads. It has thus the potential to test biomechanical hypotheses in functional morphology. Models are created by capturing the geometry (obviously one of the major inputs and an important link to VA), assigning material properties, specifying simulated forces, and imposing constraints. Models have to be validated, comparing results with in vivo or in vitro experimental data, and can be altered to examine the consequences of changes to input parameters. The output of FEA is quantitative too and mostly relates to stress, which is a measure of the amount of force per unit area; to strain, which is a measure of deformation representing the relative displacement between units in the material body; and to strain energy, which is the net potential energy stored in a solid that has been deformed by forces.

FEA is a deterministic process, i.e., the outputs of two simulations using different parameters (varying geometry, material properties, force, constraints) will always lead to different results. The problem with FEA is that there is no method to compare them in a statistical sense, e.g., how different are the results between two group average models compared to within group variation? As discussed above, geometric morphometrics can deliver a group mean configuration or a warped intermediate geometry. It can also inform about shape and form variation within groups or between groups and it can provide reconstructed input forms for biomechanics in a more reproducible way than traditional procedures can do. Nevertheless, whatever the inputs of FEA are, the outputs are most often colored images (Fig. 6) that can just be compared visually. While one observer might interpret the differences in stress and strain between models as being "almost similar," another might exclaim how different they are. The discrepancy between the mathematical physics of elastic theory, essential for mechanics, and the quite different mathematics used in shape analysis – respectively a missing mathematical bridge between them – is a major problem in biomechanical analysis of biological forms (Weber et al. 2011). A theoretical solution was published recently (Bookstein 2012), but has not yet been tested with real data. Other attempts were undertaken to make FEA results comparable between specimens and groups. However, strain

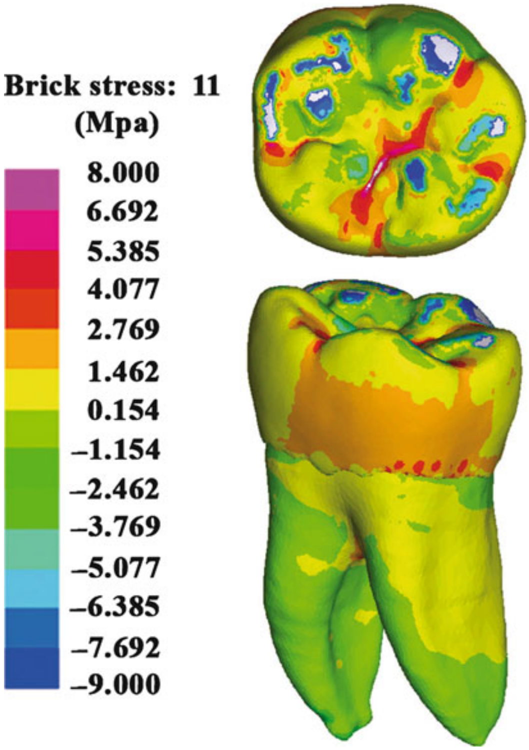


Fig. 6 Maximum principal stress distribution observed in FEA when a human molar is loaded onto occlusal contact areas (maximum intercuspation) detected by the occlusal fingerprint analysis. First row, occlusal view; second row, distolingual view. Note the high tensile stresses along the fissures (*dark areas*) (From Benazzi et al. 2011b)

frequency plots, e.g., used in a recent publication (Parr et al. 2012), cannot relate strains to the actual location (instead they just provide a summed picture of appearing strains), and landmark point strains cannot be based on semilandmarks for the mentioned mathematically incompatible differential equations. Others (Strait et al. 2009; O'Higgins et al. 2010; Wroe et al. 2010; Cox et al. 2011; Gröning et al. 2011) relied on visual comparisons between strain plots, or have tried to infer the mean of, e.g., appearing maximum and minimum principal strains, or invoked profiles along a structure of such. However, these measures only provide very scant pictures of the whole structure or sometimes involve subjective judgments. Displacement plots (O'Higgins et al. 2010; Gröning et al. 2011) again only carry information on the direction of displacements but cannot inform about the quantity of work to impose particular simulated strains.

Despite the still absent formalism to join geometry and biomechanics effectively, it can still be a step forward to simulate stresses and strains in a form. The loadings appearing on human teeth during chewing are, for instance, not well known. Recent studies (Benazzi et al. 2011b, 2013b) combining FEA and occlusal fingerprint analysis (a technique to determine actual movements from wear signals of the teeth, Kullmer et al. 2009) could show that high tensile stresses appear particularly along the fissures of the occlusal surface when realistic loading scenarios were applied (Fig. 6). Even if no big samples can be statistically compared so far, the simulations reveal important aspects that have not been considered yet, e.g., the mechanical consequences of filling fissures for protection against caries, a common dental practice. Other studies showed that the pattern of strain distribution during biting could be relatively conservative within species, regardless the actual magnitudes (Smith et al. 2014), or that certain facial geometries are not well adapted to produce high bite forces due to occurring distractive joint reaction forces (Ledogar et al. 2014). In many of those biomechanical studies, VA methods are a vital component, e.g., to virtually reconstruct a fossil form prior to FE model creation or to determine a limited set of extreme group forms to be modeled then in the FE process. Biomechanics is not part of VA but the cross-fertilizations are manifold, and innovations resulting from this combination are considerable.

Conclusion: Virtual Functional Morphology

Morphology deals with the study of shape and form of organisms and their parts. Functional morphology is the study of the relationship between the structure and the function of an organism's parts. Functional morphology is concerned with explaining how body structures such as bones, teeth, muscles, or tendons relate to different behaviors, including locomotion, feeding, defense, and reproduction. It integrates concepts from anatomy, mechanics, evolution, and development. The idea of "form follows function" in biology is an old one, for instance, expressed by Georges Cuvier (1769–1832) in his "conditions d'existence" (roughly speaking, Cuvier argued that all organismal parts that we see are already optimized toward their functional demands, otherwise the animal would not subsist). Although we have learned in the meantime that shape and form may deviate from this strong canon (genetics and theory of evolution had not been discovered at Cuvier's time), we recognize the importance of the relationship between form and function. Functional morphology is thus a fundamental approach to studying biology on a macro-level with the goal of understanding how shape and size might affect function or what the function of a structure might be at all (Rohen 2007; Lucas 2004). Such knowledge is important for developing an integrated view on biological form in the light of its function and, last but not least, it is essential to relate the phenotype with the genotype.

If we just look at the masticatory apparatus, which is certainly a key to studies in hominin evolution, the kind of unresolved fundamental questions in biology and medicine that touch closely paleoanthropology are, for instance:

- How does *variation* of skull shape relate to *variation* of mechanical loadings? At this point, we have no good data whether there is a tight relationship or not. We also do not know how the entity of a skull might compensate in one part for deficiencies in another.
- How far can geometry deviate from the mean shape to meet a given functional demand? The surviving members of a taxon were all successful despite their individual shape variation. How would a chimp, or australopithecine, or

Neanderthal, or modern human with a shape outside the 99 % sample confidence interval cope with default mechanical stresses?

- Which particular feeding behavior (which is strongly related to ecology) would make the skull shape unsuccessful? Can we predict a skull shape that would fail – given a certain behavior?
- How do the shape and mechanics of the teeth (e.g., relative cusp size, cusp relief) relate to the biomechanics of the entire skull? Can we describe patterns that make particular configurations (e.g., larger/smaller teeth, flat/high relief, protruding/retracted faces) more favorable combinations?
- What were the biomechanical consequences of the evolutionary form changes of the human skull, e.g., when jaws became smaller, the braincase grew bigger, and cranial base flexion increased?
- Depending on the result of the former question, what then could have been the feeding strategies that favored those changes, and how do they fit to what we know about related paleoecology?

We have still great difficulties to understand our evolutionary adaptations, and we do not base the treatment of patients on thorough knowledge of function in dependence of form in the field of dentistry, orthodontics, or craniofacial surgery. However, a growing number of publications are documenting a substantial progress in the development of methods, software packages, computer power, and awareness of the technologies for each field separately. Many pieces of the puzzle are already there since Schmerling discovered Engis and Darwin put evolutionary theory in place. A "virtual functional morphology" that integrates shape and form analysis with biomechanics and also considers developmental pathways controlled by genes is the next step forward for systems biology and evolutionary sciences.

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Paleopathology: Vestiges of Pathological Conditions in Fossil Human Bone

Michael Schultz and Tyede H. Schmidt-Schultz

Contents

Abstract

The methods and techniques of paleopathology are briefly described. Up to now, paleopathology has not really played a role in the field of paleoanthropology, although this relatively new science can contribute valuable facts to the reconstruction of the life of fossil humans and their antecessors. Examining the vestiges of pathological processes, the paleopathologist can reconstruct, within certain limits, the diseases early man suffered from (e.g., inflammatory and tumorous diseases) and even the hard living conditions, particularly the physical strain of everyday life. We might be able to gain substantial information about the musculoskeletal system, involved, for instance, in locomotion and work as well as some clues about possible social behavior and care (e.g., of an injured or disabled member of the social group). Not only the vestiges of pathological

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M. Schultz (✉)
Department of Anatomy, University Medical School Göttingen, Göttingen, Germany
e-mail: mschult1@gwdg.de

T.H. Schmidt-Schultz
Department of Biochemistry, University Medical School Göttingen, Göttingen, Germany
e-mail: tschmidt-schultz@web.de

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processes provide indications of how early man endured his hostile environment but also how the outcome of physical strain of everyday life can partially be reconstructed from the results of the study of the functional morphology. Therefore, selected results of a paleopathological analysis illustrating future prospects are discussed.

Introduction

Paleopathology is a research field closely related to bioarchaeology and is interdisciplinary between medicine, physical anthropology, and archaeology. This innovative scientific discipline deals with the investigation of past diseases. The wide scope of bioarchaeology which is also an interdisciplinary research field and has recently been outlined for the Anglo-Saxon World by Jane Buikstra and Lane Beck (Buikstra and Beck 2006) also suggests certain procedural methods for the future of paleoanthropology. Archaeological human skeletal remains, mummies, bog bodies, and fossil human bones are examined both with scientific and with medical methods. Human fossil remains can also be regarded as bio-historical documents because they report on the everyday life, afflictions, and illness occurring at the dawning of mankind when no written records were available. Similar to written records, fossils "can be read" in the same way that archaeological skeletal and mummified remains of peoples of the past can be. In certain cases, the biography of an individual who lived thousands of years ago can be written, of course with some limitations. In this regard, the research of a paleopathologist resembles the efforts made by forensic medical people. Frequently, according to the results of a paleopathological investigation, it is possible to reconstruct not only the health status of a past population and the nature of diseases from which they suffered but also nutrition, housing and working conditions, and geographic and climatic as well as hygienic and sanitary factors. Thus, to a certain extent, it is possible to reconstruct living conditions of human antecessors.

To date, paleopathological investigations have rarely been carried out on fossilized specimens, although this kind of research is very promising because such examinations of prehistoric and early historical skeletal remains provide highly interesting results. Therefore, this short article suggests routine inclusion of paleopathology in paleoanthropological research.

Methods and Techniques Applied in Paleopathological Investigations of Fossils

Ideally, a paleopathological investigation on fossilized remains requires distinct macroscopic and microscopic methods to establish a reliable diagnosis. All surfaces of a find have to be inspected macroscopically. The examination with the naked eye should be supported by a magnifying glass or by a low-power light microscope. To date, most human fossils investigated have been studied macroscopically (e.g., Trinkaus 1983).

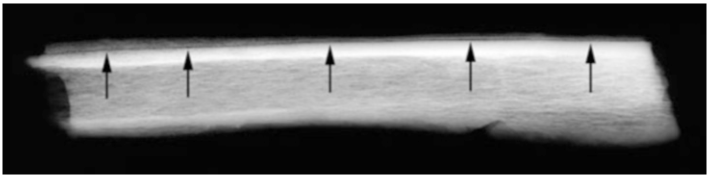

Fig. 1 Paleolithic male from Brno (Brno II). X-ray image of right ulna (anterior-posterior path of rays). Small gap (*arrows*) between the apposition and the original compact bone substance of the shaft (periostitis)

The use of a technical endoscope provides an informative basis for additional research and leads to a better understanding of morphological formations which cannot be observed by the macroscopic inspection alone. If no endoscope is available, vestiges of an inflammatory process inside the maxillary sinus can only be evaluated if a wall of the sinus is extensively broken or missing. Furthermore, an endoscopic view frequently allows a more detailed interpretation of a morphological feature because this instrument provides not only a better accessibility to a narrow space but also magnifies the feature up to 50 fold.

Conventional X-ray investigations, computerized tomography (CT), and micro-CT can add substantial information for a reliable diagnosis in paleopathology (e.g., Chhem and Brothwell 2008). Although several researchers believe that micro-CT is a noninvasive investigation, it is, indeed, only a less-invasive technique (e.g., Kuhn et al. 2007; Rühli et al. 2007). Of course, the sample investigated will not be damaged at the virtual cutting plane; however, for this analysis, it is necessary to previously remove a sample of the bone because the chambers of modern micro-CT machines are too small to hold a bone longer than a few centimeters. Therefore, micro-CT cannot be used in every fossil bone, although a true-to-life cast or a plaster complement would compensate for the loss of such a small piece of bone (cf. Schultz and Schmidt-Schultz 2014). Interpreting conventional X-ray images of fossil bones, researchers should not expect too much from such images. Postmortem loss of bone substance and secondary washing in of soil particles by water (diagenesis) might change the original bone substance such that in an X-ray image, there seem to be intra vitam changes due to disease. Furthermore, an X-ray image presenting a porotic appearance of a compact or cortical bone fragment does not allow us to diagnose, for instance, whether the bone had been affected by an inflammatory or a diagenetic process. Also osteoclastic destruction at the microlevel might not be visible in a conventional X-ray image which might lead to a false diagnosis. As an example, the Paleolithic case of the "Fossil Man from Brno II" can be mentioned. In this relatively well-preserved skeleton, among other findings, a slightly porotic bone apposition is visible on the shaft fragment of the right ulna (Schultz and Nováček 2005). There is a very small gap between the apposition and the original compact bone substance of the shaft which appears not to be affected by an osteoclastic process (Fig. 1). However, the subsequently conducted microscopic investigation of this ulna showed that the compact bone had already been destroyed intra vitam by osteoclastic resorption. This example demonstrates the shortcomings of a disease diagnosis in fossil bones using only macroscopic and radiological techniques. Another case deals with the macroscopically and radiologically (CT) established diagnosis of probable chronic anemia in the archaic *Homo sapiens* cranium KNM-ES 11693 from Eliye Springs at Lake Turkana, Kenya (Bräuer et al. 2003). Here, the nature and the location of the enormous thickening of the skull vault and the porotic structure of its external surface are typical morphological features probably characteristic of healed chronic anemia (e.g., Aufderheide and Rodríguez-Martín 1998; Ortner 2003; Steinbock 1976). Without microscopic examination, a more detailed diagnosis is not possible.

Scanning-electron microscopy and, particularly, light microscopy are useful tools for the examination of fossil bone at the microlevel (cf. Schultz 1999; Schultz and Schmidt-Schultz 2014).

Additionally, physical, molecular, and biochemical methods and techniques can successfully be carried out in paleoanthropology to diagnose diseases (cf. Schmidt-Schultz and Schultz 2014). However, to date, this research field is just getting started.

Elements of Paleopathology in Paleoanthropology

As mentioned above, in the study of human skeletal remains, various processes and activities which influenced this individual in the course of his life and provoked characteristic vestiges on bone surfaces can be detected and investigated. These activities can include everyday accomplishments, such as household chores, occupation, sports and combat, however, in particular, also diseases which lower the quality of life and diminish any positive feeling toward life. The goal of a paleopathological investigation is to explore the nature (casuistics), the causes (etiology), the frequencies, and the spread of diseases (epidemiology) in the past. These aims can also be pursued in paleoanthropology, although, as a rule, the number of cases we can observe is limited. Innovative aspects are conclusions on basic social affiliation in human antecessors. When establishing a diagnosis, researchers might act with caution because, occasionally, pseudopathology might cause mistakes (e.g., Wells 1967). Due to advanced age, particularly in fossil bones, vestiges of postmortem destruction (e.g., diagenesis) might mimic products of pathological conditions.

First Descriptions of Vestiges of Disease in Human Fossils

One of the first researchers to study human fossils was the German anatomist Hermann Schaaffhausen. He recognized, in the skull of the Neanderthal from the Kleine Feldhofer Grotte, vestiges of traumatic origin (Schaaffhausen 1859, 1888), whereas Rudolf Virchow, the famous German pathologist who, unfortunately, misinterpreted the nature of this Neanderthal noted the fracture of the left arm (Virchow 1872).

Pioneering work in this field was also carried out, for instance, by Eugène Dubois (Dubois 1896) who, for the first time in a human fossil, described an eye-catching huge bone exostosis on the left femur of the *Homo erectus* ("*Pithecanthropus erectus*") from Trinil (Java). This exostosis originated after a severe traumatic distraction of the muscles and tendons (*Myositis ossificans*) in the medial region of the left thigh (e.g., adductor muscles). Roy L. Moodie, the leading pioneer in paleopathology before World War II, reported, in several articles (e.g., Moodie 1918) and in his very innovative book dealing with animal and human paleopathology (Moodie 1923), on cases, causes, and conditions of various diseases in subfossil and fossil bones.

Selected Examples of Pathological Cases Illustrating the Potential of Paleopathology in Paleoanthropology

Since the beginning of time, the biotope has played a major role in human life, not only for human antecessors but also for the modern humans of the Early Modern Times and, in some parts of the world, right up to today. Particularly, the provision of food has stood in the foreground of all activities, and therefore, hunting was once the most widespread occupation, particularly in the times of the Neanderthals. As large animals, such as mammoths and large ungulates were predominantly hunted, there was a high risk of injury (Berger and Trinkaus 1995). This might explain the nature and the frequency of fractures (Fig. 2) observed in the skeletons of Neanderthals (e.g., Schaaffhausen 1858; Schultz 2006; Berger and Trinkaus 1995). This risk led to the comparison drawn between the fracture pattern of Neanderthals and that of rodeo riders (Trinkaus 2012). However, we cannot neglect the possibility that also, probably additionally, interhuman violence took place and might have been responsible for such traumata (Churchill et al. 2009; Zollikofer et al. 2002). Typical examples for the latter assumption are the Neanderthal cases of Shanidar 3 (Churchill et al. 2009) and St. Césaire 1 (Zollikofer et al. 2002). The adult male from Shanidar 3 shows a puncture wound in the left ninth rib (Churchill et al. 2009). Here, a lithic point had perforated the bone. Probably, the weapon would have been an arrowpoint; however, also the lithic blade of a knife or a spear point cannot be excluded (Churchill et al. 2009). The second example, the young adult individual from St. Césaire dating back to 36,000 years ago, suffered from a skull injury caused by a sharp implement which healed leaving a bony scar (Zollikofer et al. 2002). These two cases demonstrate that the highly developed Mousterian weaponry was not only used for hunting but also for combat which is, probably, a characteristic human trait.

Indeed, in paleopathology, the nature, the location, and the pattern of injuries tell us much about the locomotion as well as about occupational stress. If an individual was badly injured or hurt in some other life-threatening way, the expectation would be that there was no chance to survive. However, some Neanderthals exhibit vestiges of very severe traumata which had healed and the individuals survived for many years, however, with marked disability (Fig. 2). Such cases were, for

Fig. 2 Left ulna of the male Neanderthal from the Kleine Feldhofer Grotte. Due to fracture, wrong position of olecranon, significantly reduced radial notch, and rotation of the distal part of the ulna shaft: (**a**) lateral view, (**b**) X-ray images, *1* medial-lateral path of rays, *2* anterior-posterior path of rays

instance, the Neanderthals from the Shanidar Cave in the Zagros Mountains, Iraq (Shanidar 1; Trinkaus and Timmerman 1982; Trinkaus 1983), and from the Kleine Feldhofer Grotte, Germany (Czarnetzki and Pusch 2002; Schultz 2006). In both groups, the individuals only survived because their social group took care for them, in the case of Shanidar 1 even extensively.

The occurrence and the frequency of degenerative joint disease are closely associated with physical strain and occupational stress. This explains the appearance of osteoarthritis in Paleolithic individuals. Astonishingly, the intensity and the severity of such lesions in Paleolithic people are, as a rule, less pronounced (e.g., in the elderly male from the Kleine Feldhofer Grotte; Schultz 2006) than, for instance, in late medieval individuals. Corresponding findings are also existent in early historical hunter-gatherer populations and sedentary populations. The cause of this phenomenon is probably to be found in a frequent muscle training which allowed a more efficient muscular action leading to a more effective muscle guidance of the joints. Due to the better muscle guidance, the joint cartilage was less stressed which prevented early joint wear. Sometimes, however, degenerative joints have to be regarded as posttraumatic alterations (e.g., Berger and Trinkaus 1995).

Enthesopathies which are musculoskeletal stressmarkers (Capasso et al. 1999; Hawkey and Merbs 1995) are related to muscle function and joint strain. As a rule, they represent primarily painful disorders of muscle or tendon attachments at the bone surfaces (e.g., myotendinitis) which might heal after a while if the muscles are not strained any longer, which is not very probable in Paleolithic people who had to struggle for their lives. The kind and the location of enthesopathies in the human

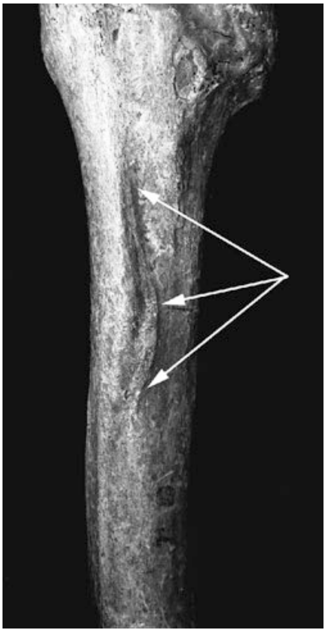

Fig. 3 Ventral view of the shaft of the right humerus of the male Neanderthal from the Kleine Feldhofer Grotte. Enlarged lateral lip of the bicipital groove (*arrows*)

skeleton tell us which muscle groups had been stressed (Fig. 3) and give clues to the nature of the physical strain which had affected the individual. Enthesopathies are relatively frequently found in Neanderthals. Principally, there are two kinds of strained tendons: (1) "osteoblastic enthesopathies," in which constant physical load enlarges the bone muscle attachments. Thus, a relatively regular surface protuberance of various sizes might originate (Fig. 3). If severe strain intensively affects the bone surface, additionally, the periosteum is stressed and micro-bleeding might occur in the region of the attachment of the tendon. After healing, the hemorrhage can be organized as connective tissue which might later ossify. In this way, the enlargement of muscle attachments can be explained. (2) "Osteoclastic enthesopathies" is a condition wherein very sudden, intermittent tractions of a muscle at the bony attachment might cause an interruption of the blood vessel supply of the bone at the microlevel which leads to a decay of the neighboring bone tissue. Thus, this tissue becomes necrotic and is eaten away by osteoclasts. A fosse will develop approximately of the size and the shape of the attaching part of the tendon which will be filled in the cause of healing by connective tissue producing a fibrous scar. After maceration (decomposition), a fosse-like cavity is left indicating physical strain. As a rule, in Neanderthals and other Paleolithic individuals, only the first group of "osteoblastic enthesopathies" described is found.

During the course of paleopathological research on human fossil remains, frequently changes on the internal skull lamina are neglected. This is probably due to the fact that researchers might not be quite aware of this kind of morphological alteration, due to intra vitam reactions of the meninges (cf. Schultz 2006), such as hemorrhages and inflammations (e.g., small epidural hematomas due to

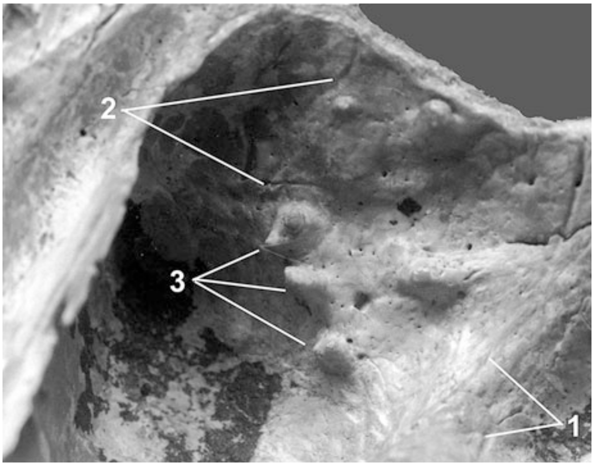

Fig. 4 Left zygomatic bone (NN 34, excavated 2000) of the male Neanderthal from the Kleine Feldhofer Grotte. View into recess of the left maxillary sinus. *1* well organized bone apposition, *2* blood vessel impressions, *3* tumor-like formations

trauma or bacterial meningitis). A reliable differentiation of the nature of such meningeal afflictions can only be established by microscopy (e.g., Schultz 2001, 2003, 2012). The elderly male from the Kleine Feldhofer Grotte exhibits changes on the internal lamina of both parietal bones which are probably the vestiges of a healed pathological meningeal process (Schultz 2006). The same individual also shows vestiges of a healed hemorrhagic or inflammatory meningeal process in the sulcus of the superior sagittal sinus of the brain.

The endoscopic inspection of the nasal cavity and the paranasal sinuses, as well as the middle ear region, provides, as a rule, interesting results also in fossil human remains. The walls of the zygomatic recess of the left maxillary sinus of the elderly Neanderthal from the Kleine Feldhofer Grotte (Fig. 4) reveal residuals of a chronic inflammatory process (Schultz 2006). Additional to the well-known features of a chronic inflammation which is expressed by coarse and sclerotic bone surfaces and some residues of abnormal, fine blood vessel impressions, there are several relatively small, pluglike, or polypoid formations (Fig. 4) which partly represent the healing stage of a small ulcer or a “pre-tumor stage” (Fig. 5a) or partly new tumorous formations (Fig. 5b). This case is particularly interesting because it is uncommon that at the bottom of such a chronic inflammatory process, tumorous growth developed. It is known from prehistoric and early historical populations that inflammatory processes of the middle ear region and the paranasal sinuses are found four or five times as frequently in individuals of the lower class as in members of the upper class (e.g., Schultz 1996). Thus, this group of diseases is called “poor people’s disease.” Probably, the most important primary cause of this kind of infection is to be found in inadequate housing conditions. Here, the smoke of the fire in the hearth probably played the major role for the occurrence of this disease. To date, for Neanderthals, we do not have sufficient information on the frequency and the intensity of chronic inflammations of the paranasal sinuses and the middle ear region which might be related to the living conditions in caves. For the male from the Kleine Feldhofer Grotte, we can assume that he ran a high risk of being

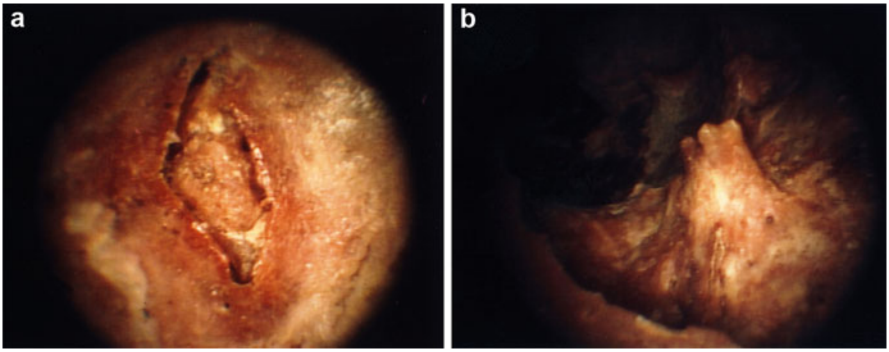

Fig. 5 Endoscopic views. Left maxillary sinus of the male Neanderthal from the Kleine Feldhofer Grotte: (**a**) bone formation which represents the healing stage of a small ulcer or a "pre-tumor stage," (**b**) small polypoid bone tumor

killed by this relapsing purulent disease (e.g., sepsis). Probably this was not the case, for the first few years after he had started to suffer from sinusitis. During this time, probably his immune system became weakened which might have contributed to his death.

Finally, in Paleolithic human remains, in a few cases, vestiges of deficiency and infectious diseases have been observed. However, as a rule, without microscopic investigations, reliable diagnoses cannot be established. Thus, only tentative diagnoses are possible. Still, some examples can be briefly mentioned. Of the group of the nonspecific stressmarkers, transverse linear enamel hypoplasias (LEH) were observed. These less-mineralized lines in the dental enamel which, in paleopathology, provide an estimation of the relative morbidity of prehistoric and early historical populations can be caused by malnutrition and infectious diseases. Such lines were found in the young adult *Homo erectus* from Dmanisi (Bräuer et al. 1995; Bräuer and Schultz 1996) and in several Neanderthals (Ogilvie et al. 1989). In Neanderthals, these lines are relatively frequently seen with 75 % (Ogilvie et al. 1989). As already mentioned above, the skull of the archaic *Homo sapiens* cranium KNM-ES 11693 from Eliye Springs exhibits morphological features which suggest chronic anemia of unknown origin to be responsible for the enormous thickening of the vault (Bräuer et al. 2003). Although CT images were available, without the results of a microscopic examination, no convincing diagnosis was possible to reliably diagnose this disease case. As an example of a rare infectious disease, we cite the *Homo erectus* cranium from Kocabaş in the western Turkish province of Denizli (Kappelman et al. 2008). The fragment of the right frontal bone shows lesions in the endocranial surface of the anterior cranial cavity which resemble the small granular impressions which are characteristic for *Leptomeningitis tuberculosa* (Kappelman et al. 2008). However, without further microscopic investigations, no reliable diagnosis can be established. A rather unconvincing case of diffuse idiopathic skeletal hyperostosis (DISH) was published dealing again with the Shanidar 1 individual (Crubézy and Trinkaus 1992). In the skeleton of this elderly male, enthesopathic osteophytes were observed in the lumbar vertebrae, in the left olecranon, both patellae and both calcanei (upper calcaneus spur). Only relatively slight osteophytic formations were found in both coracoid processes and the greater trochanter (Crubézy and Trinkaus 1992). Probably, these changes caused pain and a certain disability.

Conclusion

Paleopathology, which combines physical anthropology, medicine, and forensics, contributes substantially to the wide field of paleoanthropology as practiced today and also suggests certain methodological procedures for the future of this scientific discipline. Thus, the results of a paleopathological investigation provide information on the everyday life, afflictions, and illness occurring at the dawning of mankind. In particular, we learn about the nature of diseases of human antecessors and their health status. Furthermore, all these facts allow, of course within limits, the reconstruction of the past environment, with respect to factors such as nutrition, housing and working conditions, and geographic and climatic as well as hygienic and sanitary factors.

To reach this goal, standardized methods and techniques are suggested. For example, accurate scoring of nonphysiological changes in fossil human bones using predefined morphological features including vestiges of pathological processes should be employed to establish standards for further comparative analyses (e.g., Hawkey and Merbs 1995; Schultz 1988; Tilhaud 1994). Particularly, in diagnostics, the nature, the causes, as well as, the spread and the frequency of diseases in human antecessors should be studied comparatively as for prehistoric and early historical people. There is only the one difficulty, i.e., the low numbers of individuals available for such studies. However, it is absolutely worthwhile to start comparative work in this innovative field which will allow us to recognize certain tentative aspects which will, in turn, help to significantly enlarge our knowledge on the living conditions of human antecessors.

The practice of forensic anthropology also belongs to innovative aspects of paleoanthropological research. The cases of Shanidar 1 and 3, Kleine Feldhofer Grotte, and St. Césaire 1 demonstrate that many fossil remains might be of paleoforensic interest. Particularly the cases of Shanidar 3 and St. Césaire 1 raise the assumption that the Middle Paleolithic Neanderthal implements (or those of early modern humans) might be used as weaponry in an interpersonal behavioral context. Thus, the injury pattern observed in Neanderthals should be interpreted as resulting from a variety of causes, not just hunting. Activity-induced changes in the postcranial skeleton of human antecessors, for instance, the occurrence of enthesopathies, tell us about the nature and the intensity of locomotion and occupational strain.

Aspects of social care in Neanderthals can frequently be seen in connection with traumatic events. Examples are the cases of Shanidar 1 (Trinkaus 1983), St. Césaire 1 (Zollikofer et al. 2002), and Kleine Feldhofer Grotte (Czarnetzki and Pusch 2002;

Schultz 2006). Potentially, as for prehistoric and early historical individuals, effects of sociobiology of diseases might be studied. As particular diseases, so-called poor people's diseases (e.g., inflammatory processes in the middle ear region and the paranasal sinuses) or even gender-specific diseases can be explored. As we know from the Neolithic and younger periods (e.g., the early Middle Ages), there are apparently gender-related differences in the location and the frequency of osteoarthritis of the large extremity joints (e.g., Schultz 1996; Schulting and Fibiger 2012a, b). Seemingly, in early historic populations, sometimes an interdependence between the frequency of degenerative joint lesions and the social status of the diseased individuals as well as between female and male individuals can be observed (cf. Schultz 1996). Very probably, this will be not the case in Neanderthals. However, the distribution of osteoarthritis with regard to the sex and the age of individuals might, also in Neanderthals, provide interesting results.

Finally, we might obtain clues for the origin of diseases and the housing conditions of Neanderthals who lived, as a rule, in caves. A possible high frequency of inflammatory processes in the nasal and the paranasal sinuses, perhaps also of pathological processes in the middle ear region and even of the meninges, might be associated with life in a cave.

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Microscopic Research on Fossil Human Bone

Michael Schultz and Tyede H. Schmidt-Schultz

Contents

Abstract

The methods and techniques of light microscopy and scanning electron microscopy are briefly described, and the advantages of polarization microscopy are discussed. Particularly, light microscopy is a useful tool to diagnose fossil bone at the micro-level. Selected samples of fossilized human bones (e.g., *Australopithecus*, *Homo erectus*, *Homo neanderthalensis*, and Paleolithic *Homo sapiens*) were examined using plain and polarized light. The histomorphological findings show that microscopic research adds much to what can be found by macroscopic

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M. Schultz (✉)
Department of Anatomy, University Medical School Göttingen, Göttingen, Germany
e-mail: mschult1@gwdg.de

T.H. Schmidt-Schultz
Department of Biochemistry, University Medical School Göttingen, Göttingen, Germany
e-mail: tschmidt-schultz@web.de

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examination or by X-ray techniques. In particular, emphasis is placed on morphological structures that give clues to the taxonomy and the functional anatomy of early hominids. Furthermore, morphological structures which originated during the lifetime of the individual (e.g., individual age at death, physical strain, diseases) are explicable. Future perspectives of microscopic analyses are discussed.

Introduction

Up to now, microscopic studies of bone histology have not played a major role in paleoanthropology (see chapter "▶ The Earliest Putative *Homo* Fossils," Vol. 3). Seemingly, the scientific problem does not primarily require the information although the basic approach has the potential to open up and facilitate the informative value of an anthropological investigation on human fossil remains. Initial microscopic research studies have shown that it is possible to collect data which contribute substantial information on individual living conditions, diseases, and locomotion of early human beings. Thus, the microscopic investigation and light microscopy, including confocal laser microscopy (CLM) and scanning electron microscopy (SEM), open up a unique chance to obtain new and interesting information using innovative techniques. As a rule, such investigations are laborious and sometimes even expensive. Probably, this is the main reason why microscopic examination of fossil bones has only rarely been carried out. Furthermore, a microscopic examination often necessitates taking a sample of the fossil (e.g., for thin-ground section microscopy, scanning electron microscopy) which is an invasive technique. This leads to the loss of a certain amount of original substance which is usually, however, only small. At first sight, sampling constitutes irreversible damage. However, the missing part can be replaced by a true-to-life cast or by a plaster complement which can be stained in the same way as the original bone. Nevertheless, in the case of sampling, the necessity for such an intervention has to be carefully considered.

This contribution briefly outlines the principal methods and techniques as well as the possible benefits of a microscopic investigation on fossilized materials in paleoanthropology.

What Does Fossil Bone Represent at the Microscopic Level?

Fossils are preserved remains of past organisms (see chapters "▶ Taphonomic and Diagenetic Processes," Vol. 1 and "▶ Paleoecology: An Adequate Window on the Past?," Vol. 1). Several mechanisms are known to lie behind fossilization processes. Bony tissues might mainly be fossilized by various kinds of mineralization, such as peri-mineralization, replacement, and recrystallization. If the original tissue is completely degraded and lost, the external shape of a bone might be preserved as a cast. Interestingly, sometimes bones of respectable age, such as from Neanderthals, do not show any characteristics of a fossilization process. Thus, such a bone has only been preserved by protective conditions, for instance, by the protective climate and the shelter of a cave and still might have kept its original morphological and physical character just like fresh bone.

Using microscopic techniques, particularly with plain and polarized transmission light, the nature of a well-preserved fossil and the kind and the degree of the fossilization process can be determined. Thus, the individual micro-morphological features of lamellar bone, such as circumferential and tangential lamellae, osteons, and fragmented osteons, as well as various formations of woven bone can be clearly studied. Furthermore, structures at the cellular level of the bone tissue can be analyzed, such as the size and the shape of the lacunae of the osteocytes and their canaliculi and Howship's lacunae built by the osteoclasts. Although cells and soft tissues are degraded and lost, the morphological structures which were produced by these cells can be investigated. Also in the case of poorly preserved fossils, frequently these structures are still observable and might provide substantial information adding to our knowledge about the physical strain and diseases of man's ancestors.

Techniques Suitable for the Microscopic Analysis of Fossil Bone

Generally, any fossil sample is suitable for microscopic analysis. As a rule, pieces of compact bone provide better results than samples of spongy bone. However, the consistency of the bone and the state of preservation dictate which technique has to be applied to produce a satisfying microscopic specimen (Schultz 2001).

Principally, light microscopy will be the first choice, the "gold standard" of all microscopic methods to explore the micro-morphology of fossil bone. Scanning electron microscopy (SEM) (see chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1) including the examination with the backscattered mode of the scanning electron microscope (BSEM) gives us information on the external or superficial morphology of a sample taken (Bell 1990). Using this technique, also accurately prepared high-quality casts can be used.

The light microscopic investigation of a thin-ground section with its various techniques allows us to look into and through the deeper levels of the interior structure of the same sample. Thus, in the bright-field, in plain transmission light the general micro-morphology of a thin-ground section can be seen. Using polarized transmission light, particular bone structures, such as collagen fiber bundles, and also diagenetically caused formations, as products of postmortem bone destruction (e.g., brushite, which is a product of degradation and transformation processes of the hydroxylapatite) and secondarily originated (e.g., calcite) or secondarily submerged soil-dependent crystals (e.g., calcite, silicates, granular quartz), can be detected and analyzed. These secondary admixtures inform us about the microenvironments with which this bone was confronted during its long period of storage in the soil (Schultz 2001, 2003, 2012).

The results of fluorescence microscopy applied to fossil bone are, admittedly, relatively meager although this technique provides very interesting results in

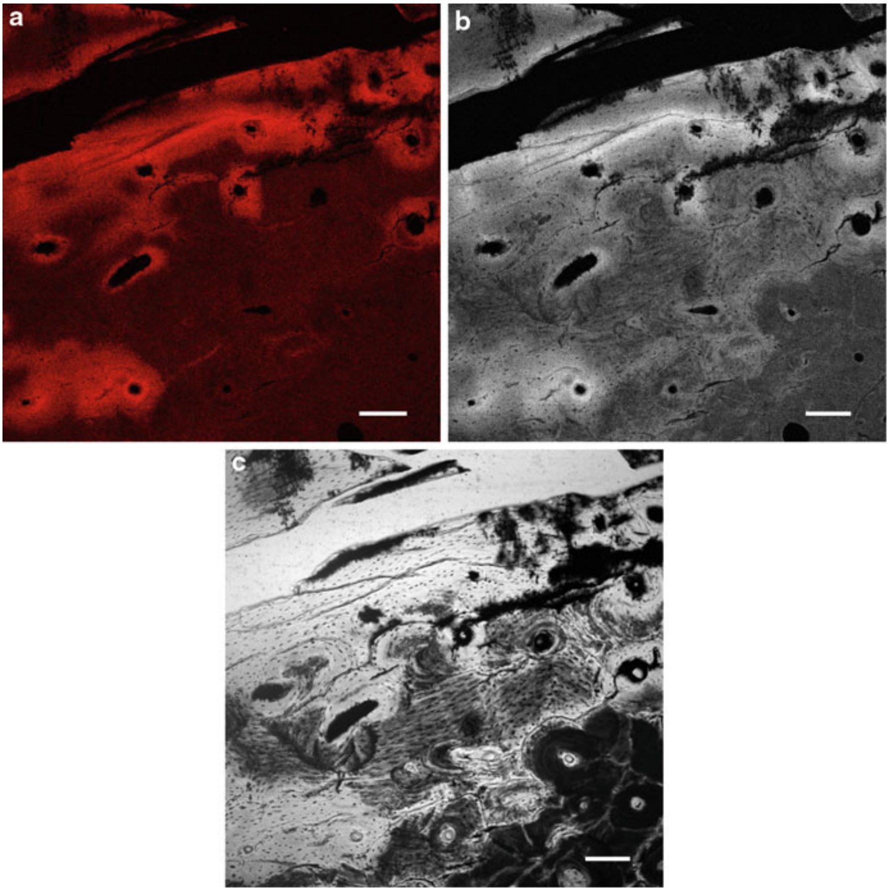


Fig. 1 *Australopithecus* from Swartkrans. Femur shaft fragment. Transverse section viewed in transmission light. Confocal laser scanning microscopic images. Bar = 0.15 mm. (**a**) Excitation of intrinsic fluorophores. Diffuse fluorescence around Haversian canals. (**b**) Grayscale image of (**a**). (**c**) Plain light image of (**a**) and (**b**). Compare different representation of morphological features and preservation state (Photos: Bernd Püschel, Department of Anatomy, University Medical School Göttingen (Germany))

archaeological bone specimens. This can also be said of the use of confocal laser microscopy (CLM) which, however, allows analysis of only one very thin level (Fig. 1) in the relatively thick thin-ground sections of 50 or 70 μm (Maggiano et al. 2006). Dark-field microscopy yields some useful results because various features might be visible (e.g., contours and cement lines as well as osteocyte lacunae of postmortem degraded osteons), which cannot be seen so clearly in bright-field microscopy.

Apart from transmission light, fossil bone samples can also be examined by reflected light. In this case, polished bone surfaces are analyzed in plain or in polarized light. However, in reflected light microscopy, only the superficial structures can be analyzed, whereas in transmission light microscopy, the deeper levels of the interior structure of the same sample can be studied. Furthermore, the morphological features examined using reflected light are usually not as clearly visible in detail.

As mentioned above, many skeletal remains of human antecessors are not really fossilized in the geological or paleontological sense (e.g., most Neanderthals; Fig. 2). Thus, their dry bony structure might be very fragile and brittle, and, as a rule, they have been pre-damaged by microfracture lines and postmortem resorption holes. Therefore, fossil bone samples should be embedded before being cut or ground (Schultz 1988, 2001).

Several techniques are available for the efficient embedment of bone samples and preparation of high-quality, large-scale thin-ground sections (Cho 2012; Frost 1958; Maat et al. 2006; Schultz 1988, 2001; Schultz and Drommer 1983). To guarantee a high-quality thin-ground section, the bone sample must be embedded properly which means that it should not be coated with but rather permeated by the embedding resin. In our experience, epoxy resins are the best suited embedding substances, for instance, Biodur® (type E12 and catalyst E1) which has a very high permeation due to its viscosity and is used in the plastination procedure developed by Gunther von Hagens (1979). For the embedding of archaeological specimens, this technique was modified (Schultz 1988, 2001) and is also suitable for the embedding of brittle fossils.

As a rule, fossilized bone samples are not stained with special substances to differentiate between various tissues because, frequently, diagenetic alterations do not allow a true stain (cf. Schultz 1988). Consequently, the same stain might produce a varying coloration of the same morphological structure (e.g., a collagen fiber bundle). Using polarized light, specific bone structures, such as collagen fiber bundles, can be viewed and analyzed, also without staining the bone sample. However, the thin-ground section should have a thickness of 50 or 70 μm since, otherwise, relevant structures are not determinable (e.g., in the case of a thickness of 10 μm, collagen fiber bundles are not observable).

What Can Light Microscopy Contribute to Paleoanthropology?

In general, most morphological features of fossil bone can be examined and studied at the micro-level in a similar way to recent fresh bone samples using thin-section microscopy. Among other features, the nature and the degree of the fossilization process can be determined, and we might learn something about the conditions of the microenvironment the bone was confronted with during its long period of storage in the soil which tells us, additionally, something about soil sedimentation (Fig. 3) and past climatic changes.

Occasionally, also fossil bone shows changes in its micro-texture due to diagenetic processes (Behrensmeyer et al. 1989; Bell 2012; Schultz 2001, 2012). This circumstance sometimes complicates the microscopic analysis but does not make it impossible. Vestiges of diagenetic processes sometimes resemble vestiges of

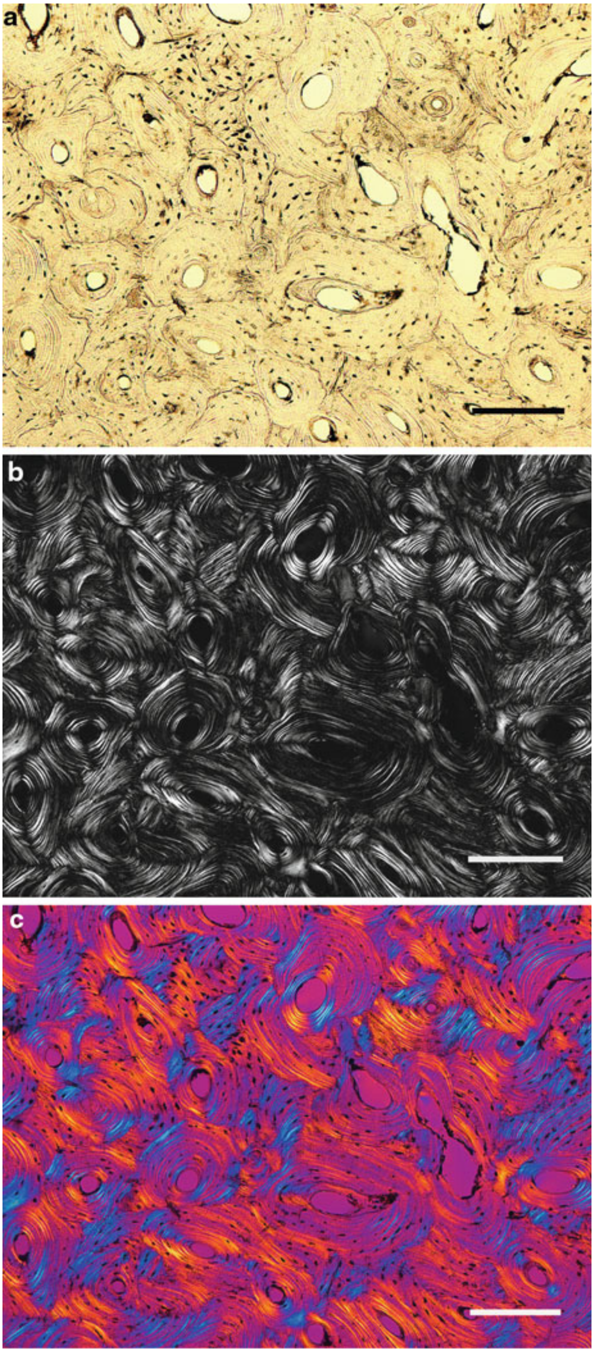
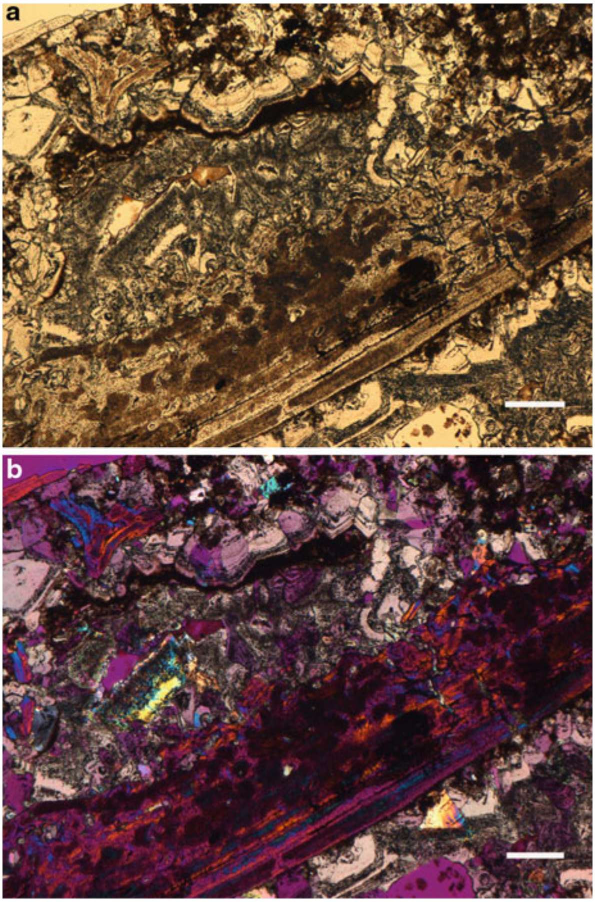


Fig. 2 *Homo neanderthalensis* from the Kleine Feldhofer Grotte. Mid-shaft of the right femur. Transverse thin-ground section viewed in transmission light. Regular compact bone structure of a mature individual. Bar = 0.2 mm. (**a**) Plain light image, (**b**) linearly polarized light image, (**c**) linearly polarized light image with λ-plate red I order

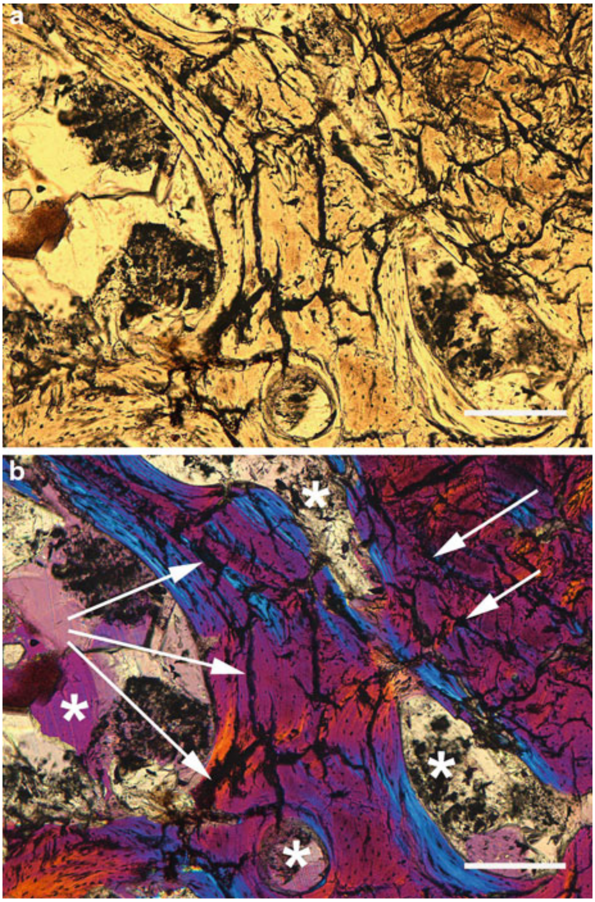
Fig. 3 *Australopithecus* from Sterkfontein (D3-STS-68). Humerus shaft fragment. Transverse section viewed in transmission light. Bar = 0.1 mm. Breccia of compact bone and surrounding stone (crystals). Bar = 0.5 mm. (**a**) Plain light image, (**b**) linearly polarized light image with λ-plate red I order



diseases (pseudopathology). However, in the majority of cases, alterations caused by disease during the lifetime can be reliably differentiated from changes caused by postmortem reactions (Schultz 1997, 2001).

Thus, processes of aging (e.g., Nováček 2012), decrease or increase of functional activity (e.g., Maggiano et al. 2008), evidence of malnutrition (e.g., Mays 2008; Ortner 2003; Schultz 2001, 2003, 2012), as well as the different structures occurring through specific and nonspecific bone inflammations (e.g., Schultz 2001, 2003, 2012; Schultz and Roberts 2002; Schultz and Teschler-Nicola 1987) can be detected. Also changes caused by metabolic diseases or circulatory disturbances (e.g., Mays 2008; Schultz 2001), the nature of bone tumors and tumorous lesions (e.g., Schultz 1986), and genetic disorders are identifiable with the aid of microscopic methods. Up to now, these methods have never been used in an extended and comparative study using the remains of fossil hominids and other Hominoidea. In the following, several examples are given to illustrate the benefit of light microscopy in paleoanthropology.

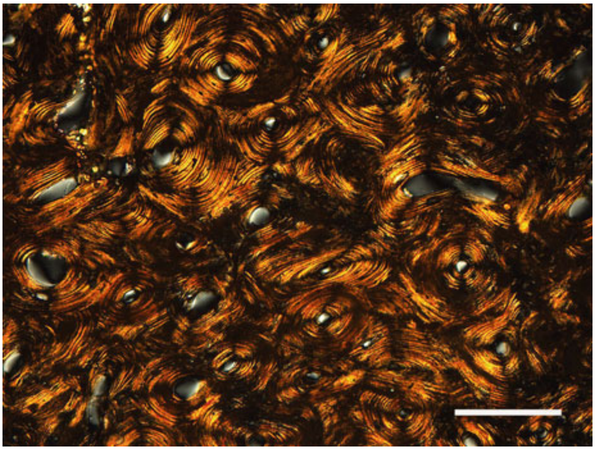
Fig. 4 *Australopithecus* from Swartkrans (SK-82). Femur shaft fragment. Transverse section viewed in transmission light. Diagenetic changes: *arrows* = postmortem microfractures due to soil pressure; *asterisk* = postmortem fill (crystals). Bar = 0.2 mm. (**a**) Plain light image, (**b**) linearly polarized light image with λ-plate red I order



Diagenetic Changes

Even fossils can show vestiges of diagenetic changes which tell us something about the microenvironment during their long period of storage in the soil (Fig. 4). Frequently, we can observe vestiges of destruction caused by soil and water, such as very fine cracks resulting from microfracture lines originated by soil pressure and products of a postmortem crystallization process (e.g., calcite crystals). Thus, newly crystallized structures can sometimes aggregate and partly break up internal structures of a bone (Schultz 1997, 2001). As a general rule, in contrast to the situation in archaeological, i.e., prehistoric or early historical, skeletal remains, we rarely see vestiges due to destruction by microorganisms, such as plant roots, fungi, algae, bacteria, or arthropods. The reason for this phenomenon is, probably, that a bone severely affected by microorganisms will completely degrade during the very long time of storage in the soil. Thus, only skeletal remains preserved in a protected environment (e.g., cave; muddy soil, ashes) have a chance to survive as a fossil.

Fig. 5 *Homo sapiens* from Preclassic Tlatelcomila, Tetelpan (Mexico, DF). Mid-shaft of femur shaft fragment. Transverse thin-ground section viewed in linearly polarized transmission light. Compact bone structure of an adult individual shows evidence of low heat influence (collagen fiber bundles show *yellowy-orange* coloration) and perimortem cut marks. Bar = 0.2 mm



Low Heat-Induced Changes

Effects of heat and fire cause typical changes in the microstructure of bony tissues (Grimm and Strauch 1959; Nováček 2012; Piepenbrink and Herrmann 1988; Schultz 2001; Wolf 1999) which are also observable in the bone collagen (Schultz 1997, 2001; Teschler-Nicola and Schultz 1984).

As investigations on prehistoric and early historical skeletal remains have shown, relatively low temperatures (below 300 °C), maintained over a longer time period, can apparently cause characteristic changes in the morphological behavior of the collagen fiber bundles seen in polarized transmission light (Schultz 1997; Teschler-Nicola and Schultz 1984). The collagen structures are colored, yellowy orange, not white as usual (Fig. 5). The cause of this phenomenon probably lies in a minimal shrinkage of the fibers.

Prehistoric bones which show this change of coloration using polarizing light microscopy are sometimes associated with the practice of cannibalism, particularly if perimortem cut marks are observable (cf. Turner and Turner 1999).

To date, no such cases are known in paleoanthropology. However, there is a femur found by Adolf Kleinschmidt at Salzgitter-Lebenstedt (cf. Hublin 1984; Kleinschmidt 1965) which shows Neanderthaloid morphology and from which a thin-ground section was prepared. In polarized light this section exhibits the feature of low heat influence (Fig. 6).

Estimation of Individual Age

The estimation of the biological age of archaeological specimens using microscopic techniques is a well-known method; however, it is not really frequently used in physical anthropology (Streeter 2012). Up to the present, this method of age estimation has not been carried out on paleoanthropological materials. The reason

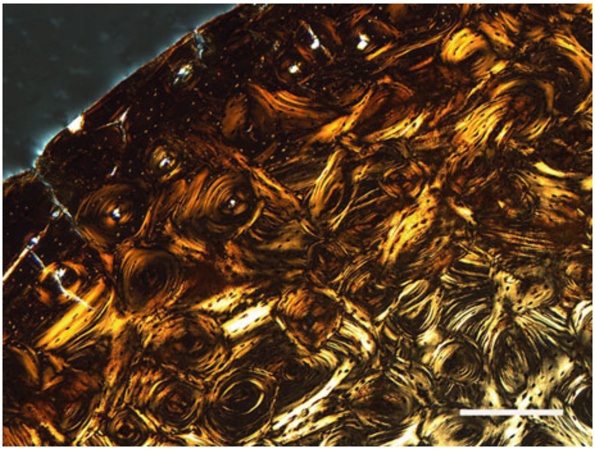


Fig. 6 *Homo neanderthalensis* from Salzgitter-Lebenstedt. Distal third of shaft of the right femur. Transverse thin-ground section viewed in linearly polarized transmission light. Compact bone structure of an adult individual shows evidence of low heat influence (collagen fiber bundles show *yellowy-orange* coloration). Bar = 0.2 mm

probably lies in the fact that, to date, we do not have age-determined specimens available for comparison purposes. Two different methods are used to estimate microscopically biological age in the postcranial skeleton: (1) the histomorphometrical method (HMM) and (2) the histomorphological method (HML). The HMM method which was introduced by the forensic anthropologist Ellis R. Kerley is applied to long tubular bones (Ahlquist and Damsten 1969; Drusini 1987; Kerley 1965; Kerley and Ubelaker 1978; Robling 1998; Uytterschaut 1985, 1993). However, also other parts of the human skeleton can be used, such as clavicle sections (e.g., Stout 1989; Stout and Gehlert 1980; Stout and Stanley 1991; Stout et al. 1996; Stout and Paine 1992). The application of this method is based upon the frequencies of osteons (Haversian systems), fragmented osteons (interstitial lamellae), non-Haversian canals, and the percentage of the external circumferential lamellae (Kerley 1965). The HML method is based upon the morphological nature (presence, size, shape, development) of the following features: external and internal circumferential lamellae, osteons, fragmented osteons, and non-Haversian canals (Nováček 2012; Schultz 1986, 1997; Wolf 1999).

Possible Taxonomic Changes in Bone Morphology at the Micro-level?

Microscopic analyses of thin-ground sections taken from long tubular bones of *Homo sapiens* and *Homo neanderthalensis* show no differences in the morphology of the compact bone substance. Indeed, there are slight morphological differences between *Home erectus* and *Homo sapiens* and *Homo neanderthalensis*. In *Homo erectus*, the relatively small, regularly rounded and densely packed osteons have a relatively narrow canal. In *Australopithecus*, the difference to *Homo sapiens* and *Homo neanderthalensis* is evident (Fig. 7). The external circumferential lamellae are very thick. The small osteons are regularly rounded, are densely packed, and

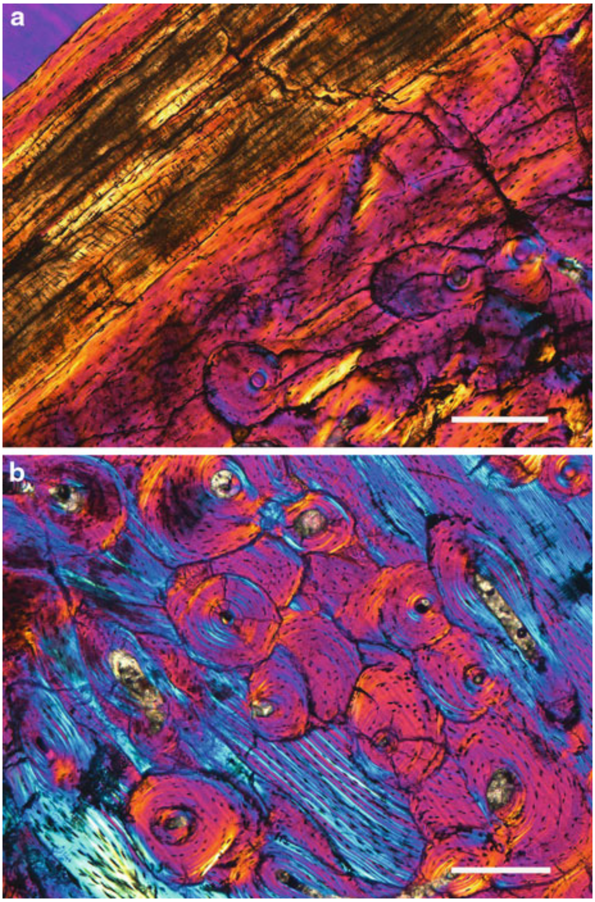


Fig. 7 *Australopithecus* from Swartkrans (SK-82). Femur shaft fragment. Transverse section viewed in linearly polarized transmission light with λ-plate red I order. Bar = 0.2 mm. (**a**) External circumferential lamellae, (**b**) osteons

have a narrow canal (Schultz 1999). The structure of the compact bone substance slightly resembles that which can be observed in *Pan paniscus* (Schultz 1999). Thus, micro-morphological features of bone are of value for additional information in taxonomic analyses.

Functional Activity and Locomotion

It is well known that locomotion and special functional activity influence the musculoskeletal system as well as functional inactivity (cf. Maggiano et al. 2011). Therefore, in bones, activity hypertrophy and inactivity atrophy can be studied at the micro-level to yield information on locomotion (see chapter "▶ Origin of Bipedal Locomotion," Vol. 3) and the use of particular parts of the skeleton. Although microscopic studies have rarely been carried out, the results of such an investigation might sometimes shed some light on the life of our ancestors. For instance,

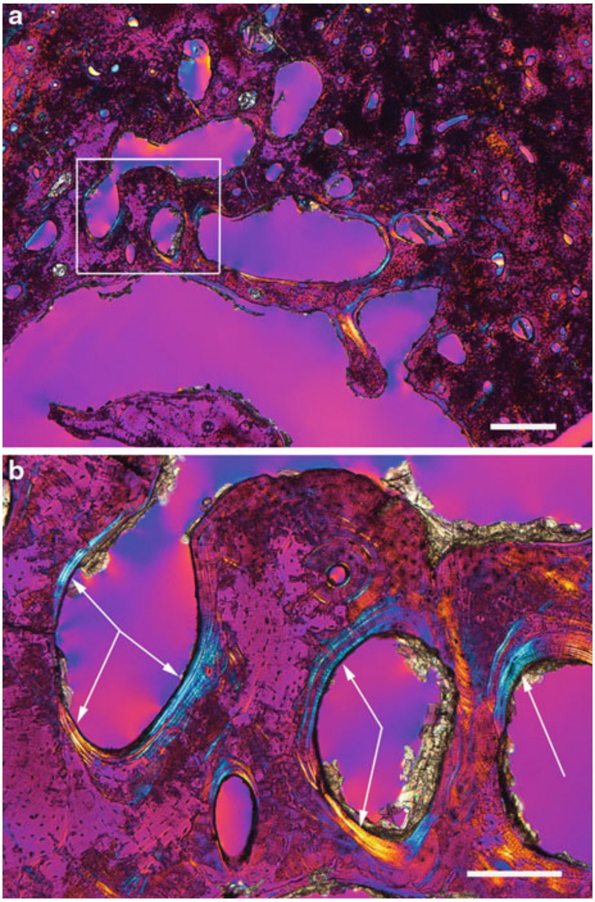


Fig. 8 *Homo neanderthalensis* from the Kleine Feldhofer Grotte. Proximal third of the shaft of left ulna. Transverse thin-ground section viewed in linearly polarized transmission light with λ-plate red I order. (**a**) Osteoporosis caused by inactivity atrophy. Bar = 0.5 mm. (**b**) Detail of (**a**) (frame); resorption holes with their own lamellar walls (*arrows*) indicating no active osteoclastic process. Bar = 0.2 mm

the Neanderthal from the Kleine Feldhofer Grotte, whose left ulna was broken many years before his death, exhibits large resorption holes at the micro-level in the primarily fractured bone (Schultz 2006). These holes are situated in the compact bone substance closely to the medullary cavity and have their own lamellar walls (Fig. 8). Additionally, the left humerus which is more gracile than the right bone shows porotic structures as vestiges of inactivity atrophy, at the micro-level, which are, however, not as pronounced as in the left ulna. These holes were responsible for the already macroscopically visible bone porosity at the transverse section level. They represent resorption holes due to the inactivity atrophy induced by the disability of the left arm after the fracture. As the margins of the holes are smooth and covered by a special regular lamellar wall, it was, indeed, an old process which the individual survived for many years.

Additionally, there are also other morphological features visible at the micro-level (e.g., tangential lamellae) which are due to inactivity atrophy (Schultz 2001, 2003, 2012).

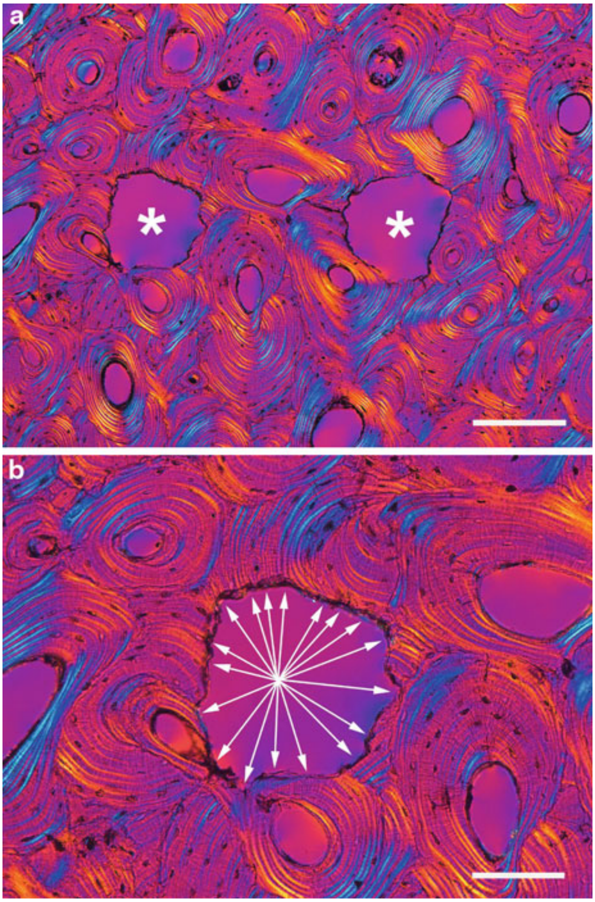


Fig. 9 *Homo neanderthalensis* from the Kleine Feldhofer Grotte. Mid-shaft of the right humerus. Transverse thin-ground section viewed in linearly polarized transmission light with λ-plate red I order. (**a**) Two large resorption holes (*asterisk*); bar = 0.2 mm. (**b**) Detail of (**a**); resorption hole with numerous Howship's lacunae (*arrows*) indicating an active osteoclastic process. Bar = 0.1 mm

Diseases and Disorders

Finally, vestiges of various diseases and pathological conditions and disorders can be diagnosed in fossil remains using microscopy. Unfortunately, paleopathology has not yet really been discovered in the wide field of paleoanthropology. Some case studies are already available, usually dealing with macroscopic findings (e.g., Trinkaus and Zimmerman 1982). An etiological or epidemiological investigation of population groups using microscopic techniques to obtain reliable diagnoses is still missing.

In summary, it would be worthwhile analyzing the following groups of diseases: evidence of malnutrition (e.g., scurvy, rickets), inflammatory bone diseases, bone tumors and tumorous lesions, and genetic disorders. However, also vestiges of the onset of disease can be detected using thin-section microscopy. As an example, the Neanderthal from the Kleine Feldhofer Grotte should be mentioned again (Schultz 2006). This mature male exhibits a frequent occurrence of irregular resorption holes (Fig. 9) in the compact bone substance of the humeri, ulnae, and femora.

The margins of these holes show many Howship's lacunae which are proof of an increased activity of osteoclasts. Probably, these changes are not normal. They might indicate the onset of a malignant process of unknown origin.

Conclusion

Microscopy, particularly the light microscopic investigation of the bones of man and his antecessors, can contribute not only ample information on the fossilization process and diagenetic circumstances, but also on heat-induced changes, functional activity and locomotion, disabilities, diseases and physical disorders, and, within limits, the individual age and even taxonomy.

For the future, microscopy could become a powerful tool which should be handled with the necessary responsibility because each sampling is an invasive intervention. The fact that a sample taken can be replaced by a true-to-life cast or a plaster complement should make this sampling more acceptable.

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Investigation on Extracellular Matrix Proteins in Fossil Bone: Facts and Perspectives

Tyede H. Schmidt-Schultz and Michael Schultz

Contents

Abstract

For several years, it has been possible to detect typical extracellular matrix proteins (ECMs), such as osteopontin, osteonectin, and osteocalcin, in archaeological bone. Additionally, it has proven possible to detect growth factors and hormones (e.g., TGF-β, BMP-2, gonatropine), bone matrix proteins of the immune system (e.g., IgG, IgA, interleukine), and biomarker for diseases, such as tumor markers (e.g., PSA, PSA/ACT) or typical molecules characteristic for nonspecific infectious disease (e.g., TNF-α, IFN-γ) and specific infectious diseases (e.g., from *Mycobacterium tuberculosis*, Ag 85), in dry (macerated) bone. Now, we are able to detect these ECMs in fossil bone as well. Thus, evolutionarily old molecules, such as BMP-2, albumin, and matrix-gla-proteins (MPG), can be detected in fossil bone of various specimens (e.g., *Anancus arvernensis*) and compared to each other and to recent specimens. Furthermore, the bone matrix

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T.H. Schmidt-Schultz (✉)
Department of Biochemistry, University Medical School Göttingen, Göttingen, Germany
e-mail: tschmidt-schultz@web.de

M. Schultz
Department of Anatomy, University Medical School Göttingen, Göttingen, Germany
e-mail: mschult1@gwdg.de

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protein patterns of childhood and adulthood (at the date of death) in the same individual can be compared, providing us with information on changes of living conditions during the individual's lifetime. Finally, the future possibilities of the study of ECMs in fossil human species are briefly outlined.

This contribution hopes to attract interest in newly available methods of biochemical and, in particular proteomic, research in paleoanthropology. These have potential to provide insights toward a better understanding of the evolution of mankind.

Introduction

Among the vertebrate organ systems, bone is unique in both structure and function. Bone is a biphasic system, consisting of an organic matrix in intimate contact with a microcrystalline mineral phase. Bone is a highly dynamic tissue that has evolved over millions of years under gravitational stress to provide mechanical support for both locomotion and protection, to serve as a calcium reservoir for mineral homeostasis, and to support hematopoiesis (Einhorn 1996). Proteomics evaluation involves the detection and characterization of the protein components of cells and tissues by partial sequence analysis and database matching.

Living bone consists of about 2 % cells and more than 90 % calcified tissue, the extracellular matrix (ECM). In contrast to other organic materials, bone tissue has a better chance of being preserved over a long time span after death due to its durability and resistance to decomposition and diagenesis. Conditions within the compact bone structure, which might be also characterized by the relatively low water content (ECM of bone 5–10 % water, in contrast a living cell contains 70 % water) and degradation enzymes, are favorable for the preservation of bone proteins (Clarke 2008). ECM proteins of the living bone bind very tightly to hydroxyapatite and/or to collagens. The apatite in which the proteins are embedded provides considerable protection against the destructive effects of temperature and chemical agents after death (Schweitzer et al. 1994).

In well-preserved bones, for many thousands of years after death, the ECM proteins are sometimes conserved as in fresh bone tissue (Fig. 1). The most serious problem to overcome is to extract and solubilize these proteins, for only if the proteins are solubilized it is possible to conduct the separation by electrophoresis, and only then it is possible to identify the proteins by so-called Western blot or mass spectroscopy.

Which ECM Proteins Can Be Detected in Ancient and Fossil Bones?

The ECM of bone consists of 65 % inorganic molecules such as calcium phosphates and about 35 % organic molecules, most of them proteins. Of these organic molecules, 90 % are collagen type 1 and only 10 % are non-collagenous proteins. These 10 % of non-collagenous proteins of the bone ECM have a tremendous

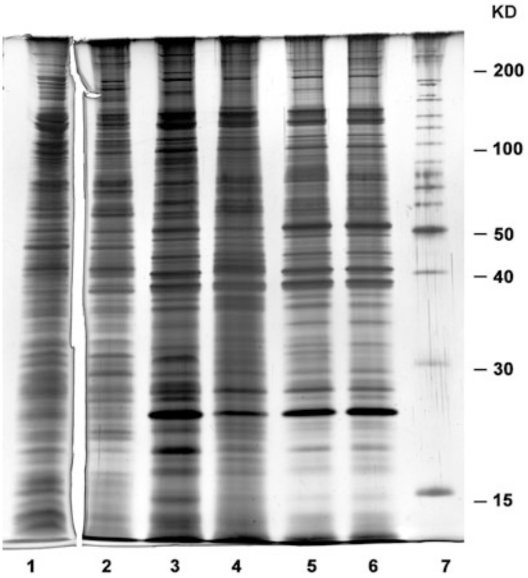

Fig. 1 1-D electrophoresis of human ECM proteins from compact bone and tooth dentin stained with silver. Lane 1, recent compact bone (right femur), male body donator, 38 years old, Department of Anatomy, University of Göttingen (Germany); lane 2, dentin (tooth 31), juvenile male, recent case, Department of Dental Medicine, University of Tübingen (Germany); lane 3, compact bone (right femur), female, 21–25 years old, Barbing (Germany), early Middle Ages (450–750 AD); lane 4, dentin (tooth 13), female, 21–25 years old, Barbing (Germany), early Middle Ages (450–750 AD); lane 5, compact bone (left femur), male, 30–39 (45) years old, Basta (Jordan), Late PPNB (7500–6000 BC); lane 6, dentin (tooth 27), male, 30–39 (45) years old, Basta (Jordan), Late PPNB (7500–6000 BC); lane 7, molecular weight marker

diversity, and many of them belong to several groups of the extracellular signaling molecules known as cytokines. Growth factors are responsible for differentiation and proliferation of cells, for example, transforming growth factor-ß (TGF-β) or bone morphogenetic protein (BMP) or erythropoietin (EPO) (Centrella et al. 1994). Another group is the interleukines (interleukine-1 [IL-1], interleukine-6 [IL-6], or tumor necrosis factor-a [TNF-α]), which have a special function in immune defense and inflammatory processes (Waage et al. 1989). A further group are the interferons (IFN), involved in defense against viruses, inhibition of proliferation, and in the apoptosis process (Sen 2001). The last group of cytokines is represented by proteins that are more involved in migration and chemotaxis of cells (Baggiolini et al. 1997). Some of these cytokines (TGF-β, BMP-2, TNF-α, IGF-II, IL-1β, IL-6, IFN-γ) can also be detected in bones from archaeological sites (Schmidt-Schultz and Schultz 2005, 2010). Also other typical bone proteins, such as osteopontin, osteonectin, osteocalcin, alkaline phosphates, and bone sialoprotein, have been identified in recent bone and bones from archaeological sites (Schmidt-Schultz and Schultz 2004, 2007). Thus, paleoproteomic research can provide results which cannot be

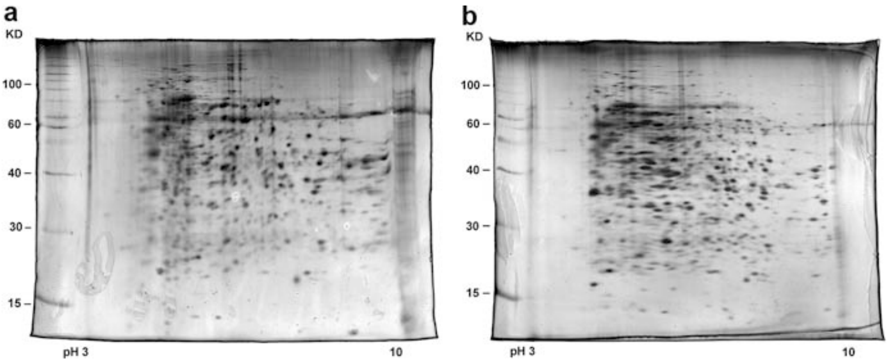

Fig. 2 2-D electrophoresis of specimens from the Late PPNB. First dimension IPG strip pH 3–10; second dimension, SDS-Page (12.5 % T, 2.5 % C), stained with silver; left-hand side: molecular weight marker. (**a**) ECM proteins from compact bone, (left femur), male, 30–39 (45) years old, Basta (Jordan), Late PPNB (7500–6000 BC); (**b**) ECM proteins from dentin (tooth 27), male, 30–39 (45) years old, Basta (Jordan), Late PPNB (7500–6000 BC)

achieved by the examination of ancient DNA. Osteopontin, osteonectin, and BMP-2 were extracted and identified in Western blots using special antibodies in a 3.4 million-year-old pre-mastodon, *Anancus avernensis* (Schmidt-Schultz et al., manuscript in preparation). Recent investigations have shown that the number of different bone matrix proteins in recent native bone is much higher than thought before: 3,038 unique proteins were identified in bone samples of four individuals (Alves et al. 2011). In three out of four bone samples, a total of 1,213 proteins were present (Alves et al. 2011). Out of these, 1,051 non-collagenous proteins could be quantified (Alves et al. 2011). Also, for only the non-collagenous proteins, this is an extremely high number of ECMs. Therefore, chances are that also in ancient and fossil well-preserved bone samples, an adequate number of proteins might also be detected. Paleoproteomic analyses thus appear to have a high potential.

Different ECM-Protein Pattern in Childhood and Adulthood

It is interesting that there is an apparent difference between the protein patterns of bone and of teeth stemming from the same individual (Fig. 2). Additionally, by creating a MatchSet with PDQuest 7.2, in which the protein spots from the different gels are matched to each other, a comparison was done that shows clearly the differences of the nature of the ECM proteins in two age sets from the same individual. Only 16 % of protein spots in the tooth were also found in the bone of this individual (Schmidt-Schultz and Schultz 2007); but the total number of spots in the 2-D gel of bone or teeth were almost the same, adding up to about 330 (Fig. 2). This can be explained by the fact that dentin normally does not undergo remodeling in the way that bone does (Borggreven et al. 1994; Cloos and Jensen 2000; Silva et al. 2004). However, also in the various kinds of bone substances, the turnover in cortical bone (i.e., compact bone substance, e.g., from the femur shaft) per year is between 2 % and 3 % (Clarke 2008) and 4 % (Parfitt 1994), while in trabecular bone turnover, it is 28 % per year (Parfitt 1994). For the turnover rate in cortical bone of small (e.g., vertebral bodies, carpal and tarsal bones) and flat bones (shoulder blade, ribs) as well as in permanently existing woven bone structures (e.g., linea aspera, upper ventral iliac spine, deltoid, and gluteal tuberosity), no reliable data are available. But for all that, remodeling rates do not play a major role in maintaining the character of the ECM because all bone ECM proteins are constantly reintegrated into the bone matrix. Thus ancient and, particularly, fossil bones represent a biological archive of ancient life.

Impact of Disease-Connected ECMs

Disease-connected molecules are another interesting field in the investigation of fossil bone. Currently, two different kinds of formation processes are known:

1. During the course of a certain disease, specific molecules are as a rule synthesized in high amounts by the diseased organism. For instance, over the life of an existing malignant tumor of the prostate (prostate carcinoma), prostate-specific antigen (PSA) which is a 30 kDa protein (complexed with a 1-antichymotrypsin 75 kDa), is secreted by the human prostate. Through mechanisms still unknown, PSA is released from the prostate into the blood circulation and ends up in the ECM of bone. The leakage of PSA is promoted by tissue abnormalities provoked by prostate cancer. PSA has been detected in the bone ECM of a 2,700-year-old Scythian king from Arzhan (Siberia, Russia) who suffered from and probably died by a metastasizing carcinoma of the prostate (Schultz et al. 2007; Fig. 3). In this case, the diagnosis “prostate carcinoma” could be established independently and confidently by combining the morphological (gross morphology, histology) and biochemical (proteomic) investigations.
2. Another possibility is to search in macerated bone for molecules that were secreted by pathogens during the lifetime of the diseased organism. For example, *Mycobacterium tuberculosis* secretes in infected individuals the complex antigen 85 (Ag 85), composed of a family of three highly homologous 30–31 kDa proteins: Ag 85A, Ag 85B, and Ag85C. Each of these Ag85 is associated with mycolyltransferases activity in vitro (Belisle et al. 1997) suggesting the essential involvement of the characteristic cell wall of the *Mycobacterium*. Ag 85 could be identified in skeletons from Siberian Arzhan, Russia (700 BC), and from Kirchberg, Germany (tenth–twelfth century AD) (Schmidt-Schultz and Schultz 2014, in press). During the course of this study, a positive control was performed in a recent human bone sample from the pathology collection of the University of Göttingen (Schmidt-Schultz and Schultz 2014, in press).

Very probably, such a diagnostic procedure would also work in fossil human bones. As several authors have shown, ECM-peptides can successfully be detected in nonhuman fossil bones (Schweitzer et al. 2011).

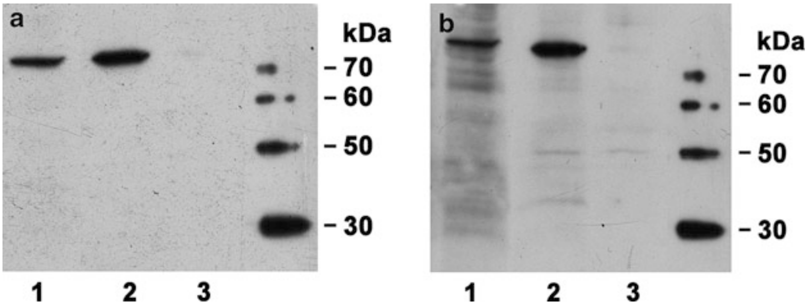

Fig. 3 Western blot. (**a**) Monoclonal antibodies against prostate-specific antigen (PSA). Lane 1, ECM proteins from left tibia of the Scythian ruler from Arzhan, 40–45 years old, early Iron Age (approx. 700 BC); lane 2, ECM proteins from right femur of a recent male body donator, 62 years old, Department of Anatomy, University of Göttingen (Germany), with known diagnosis prostate cancer; lane 3, ECM proteins from right femur of a recent male body donator, 74 years old, Department of Anatomy, University of Göttingen (Germany), not suffering from prostate cancer; right-hand side, molecular weight marker. (**b**) Monoclonal antibodies against PSA complexed with α1-antichymotrypsin (PSA/ACT). Lane 1, ECM proteins from left tibia of the Scythian ruler from Arzhan; lane 2, ECM proteins from the right femur of a recent male body donator, 62 years old, Department of Anatomy, University of Göttingen (Germany), with known diagnosis prostate cancer; lane 3, ECM proteins from the right femur of a recent male body donator, 74 years old, Department of Anatomy, University of Göttingen (Germany), not suffering from prostate cancer; right-hand side, molecular weight marker

Conclusion

Comprehensive knowledge of bone matrix components is a prerequisite for understanding the biochemistry and the physiology of bone. This basic knowledge is also necessary to discuss successfully the nature and the state of particular diseases that may have affected bones in ancient times. This interdisciplinary approach offers a good opportunity to gain more insights into the molecular paleopathology of fossil human bones. Additionally, newly developed techniques allow us to extract, to solubilize, and to detect bone matrix proteins in ancient and even fossil bones. Thus, in the near future, it will be possible to answer questions dealing with many aspects of ancient living conditions, such as aging and maturing, weaning, various diseases and the capacity of the immune system, genetically caused pathological conditions, and nutritional problems, via the examination of macerated bones

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Images in Paleoanthropology: Facing Our Ancestors

Stefan Schlager and Ursula Wittwer-Backofen

Contents

Abstract

Images in paleoanthropology are of persuasive power, since they try to illuminate ancient life which is not otherwise visually documented. The scientific community, as well as public media and museums, aim to establish a window into the past in part through visualization of scenarios from prehistoric life and

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S. Schlager (✉) • U. Wittwer-Backofen
Department of Anthropology, Faculty of Medicine, Freiburg University Medical Center,
Albert-Ludwigs-University Freiburg, Freiburg, Germany
e-mail: Stefan.schlager@uniklinik-freiburg.de; ursula.wittwer-backofen@uniklinik-freiburg.de

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environments. The role of human ancestors in these settings is captured by body and especially facial reconstructions, which comparatively easily attract attention among nonscientific audiences and therefore raise public understanding of a complex field of research, allowing it to compete successfully with other, at times more tangible scientific subjects. Within the scientific community itself, reconstructions of early hominids play only a limited role, merely supplementing a whole range of field and laboratory research, evolutionary hypotheses, and the analysis of empirical data. Paleoanthropologists and paleontologists are aware of the interpretative character of facial reconstructions that go beyond the limited set of primary facts documented in the fossils themselves.

The visual approach to paleoanthropology has changed strongly over time, varies with the media used, and depends on how we imagine our ancestors in coeval context. On the one hand, evolutionary theories and contemporary social ideas are influencing and shaping how we view and depict our ancestors. On the other hand, hominid reconstructions themselves, in turn, can influence our view and the underlying ideas.

This chapter reflects on the development of facial reconstructions over time, along with influences such as the development of methods and techniques – from drawings to manual modeling to virtual 3D reconstructions. For exemplification, special emphasis will be put on Neanderthal reconstructions, as these are linked both to early attempts at facial reconstruction and to the subsequent methodological development of reconstruction techniques during the twentieth century. Starting with the first hominid fossils found, we trace the “evolution” of facial reconstructions of Neanderthals, in order to highlight contemporary perceptions and limiting factors in the visualization of our ancestors.

Introduction

The human face is among the most popular themes of all time. It delivers uniquely fascinating images. The capability of deriving important information from the human face, such as intentions, emotions, and personality, is one of our prominent evolutionary achievements. Human ethology shows a keen interest in this highly specialized part of the human body, as it significantly enables social interactions between sender and receiver in communication (Landau 1989; Sütterlin 2013; Eibl-Eibesfeldt 2007; Grammer and Oberzaucher 2006).

The central social importance of the human face may have contributed to the wide efforts to create faces based on the fossil hard tissue remains of human ancestors since the beginning of research into fossil bones itself, e.g., the finding of the Neanderthal specimen of 1856. Motivated also by the emergence and reception of Darwin’s evolutionary theory 3 years later, illustrators and sculptors began to create a broad variety of artistic representations (Voss 2009; Larson et al. 2009). In turn, the images they created began to exert influence on evolutionary theory itself, due to their persuasive power (Prodger 2009; literature overview in Sarasin and Sommer 2010). Intensive multidisciplinary research in this field during the last decade has shown the wide range of artistic intentions and imaginations evident in the images presented to the eyes of the beholder. Thus influenced, beholders will then engage their own imagination (Eibl-Eibesfeldt and Sütterlin 2008; Henke 2010; Voss 2007).

Right after the first fossils of human ancestors began to be studied, paleoanthropological research and education generated a huge number of reconstructions, both of entire bodies and of faces. These started to replace the former, generic natural sceneries, as found in Darwin's oeuvre, by focusing on the anatomy of early hominid taxa. The visualization of human ancestors via reconstructions, allowing face-to-face confrontation, came to be a widely accepted device.

Paleoanthropological research has revealed a high degree of specialization in the facial skull, including adaptations of dentition, the vocal tract, midfacial geometry, and the orbital region to specific environmental factors. As facial soft tissues depend on craniofacial shape, the face as well as the underlying craniofacial bone structures can be assumed to be sensitive to environmental conditions, and thus are helpful to consider in paleoecological interpretations. However, it should be noted that only the large mastication-related muscles leave visible markers, whereas the shape and size of muscles responsible for facial expressions cannot be estimated from the remaining bone material.

In sum, in addition to the general, inherent attraction of pictures representing an extinct world, due to our ethological interest in faces, facial reconstructions of our ancestors are of special attractiveness to the public as well as to the scientific community.

But does facial reconstruction really fulfil the scientific criteria to be regarded as a legitimate window into the past? Are facial reconstructions of our ancestors strictly a result of manipulating "facts" and hence nothing more than an objective visualization of those facts?

There are several arguments which cast doubt on this assumption. For one, paleoanthropological reconstructions try to capture the hitherto unknown appearance of extinct human taxa, whether or not their faces resembled ours. However, humans are inherently sensitive to variations in physiognomic appearance in their species and prefer individuals who are similar to themselves. Even given a set of modern methods which try to achieve standardization, and despite deliberate efforts towards objectivity, it is not possible to overcome this bias. Modern reconstructions have an immanent intention to attract and emotionally reach the beholder. This can be achieved to a maximum degree with faces similar to the beholder.

Thus, the well-known, clearly established "cross-race" effect is an unavoidable factor influencing reconstruction results. Psychological research on perception has shown that identification, recognition, and interpretation of human faces is much more successful with faces belonging to the perceiver's own ethnic group, compared to out-group faces (Meissner and Brigham 2001; Sporer 2001).

A typical manifestation of this phenomenon can be seen with reconstructions of Australopithecines or early hominids that have been given white sclera, in contrast to models of non-human modern primates, which are mostly equipped with brownish sclera. According to the cooperative eye hypothesis, humans are especially reliant on gaze-following in social situations; the hypothesis suggests that eyes developed a new social function in the course of human evolution, most likely to support cooperative social interactions (Tomasello et al. 2007). In actuality, white sclera may have evolved much later in the hominization process than suggested by the respective reconstructions but, presumably since they make gaze-following easier, white sclera are more pleasant to look at for the human beholder than brown sclera.

Facial reconstructions of unidentified bodies in forensic anthropology, which can draw on better methodology with respect to the thickness and texture of soft tissue layers compared to paleoanthropological reconstructions, have shown an unavoidable tendency to implement familiar facial features, regardless of the ethnic origin of the dead. This is owed to the fact that these traits are familiar to the person executing the reconstruction. The effect can be expected to be even more pronounced in the case of extinct taxa, where less reliable information is available and a wide range of prejudices interacts with scientific approaches (Schmölders 1995).

Recent reconstructions of hominids tend to personalize, trying to appeal to the beholder by evoking the notion of an individual's fate. Since neither destiny nor fate of the respective hominid specimens are known, this represents an interpretation. While scientists might agree on a reconstruction's general anatomical features, texture details – such as eye, hair, and skin color – or aging traits largely lack scientific foundation. The concept of population variability has replaced obsolete typological definitions of modern human populations, a development that has been discussed intensively by anthropologists over the last decades. Little, however, is known about the facial phenotypes of human ancestors. The more details are modeled, the more "realistic" a reconstruction seems to be. But in the absence of knowledge about anatomical variability at the population level, the opposite is true.

Whether the set of depicted traits ever existed in a real phenotype, or whether they fit into the range of variability, cannot be answered based on the inherent features of the material. Hublin (2007) summarizes this dilemma as follows: "'Scientifically based' reconstructions of fossil hominids filling the museums in Europe and America may say much more about our way of perceiving human diversity than about the actual aspect of these hominids. In this respect, the progress of our reconstructions since the beginning of the twentieth century may be more limited than is often assumed" (Hublin 2007, p. 825).

However, the media in which reconstructions are presented serve different functions, and therefore reconstructions are introduced differently in different settings. Within the scientific community of paleoanthropologists, reconstructions are more cautiously employed than in media of public interest, where they often are the items of central interest. The recently issued second edition of a textbook titled *Our Origins* (Larsen 2011) addresses students and lecturers in physical anthropology; it successfully manages to explain evolutionary processes within around 500 pages, richly illustrated by numerous concrete figures, but includes very few facial reconstructions, demonstrating just general types. Museums, on the other hand, which legitimately aim to interest the broad public in our history and, accordingly, try to offer immediate experiences, surpass each other with individualized reconstructions of early hominids, sometimes using dermoplastic materials that mimic human skin (as is the case, e.g., with reconstructions created by Elisabeth Daynès, John Gurche, and Alfons and Adrie Kennis) or applying forensic methods (Senckenberg Natural History Collection Dresden 2011; see http://www.demografische-chance.de/mitmachen/forschungsmuseen-erklaeren-den-wandel/senckenberg-naturmuseum.html). This individualization, however, hides the diversity of phenotypes that is known to have existed, and thus limits the viewer's appreciation of the complex mechanisms of environmental adaptations and interactions.

Apart from reconstructions of this type, produced mostly by scientists or by institutions claiming to be educational, a large variety of popular representations exist, including science fiction and cartoon artwork. These renditions, however, which claim little if any allegiance to scientific facts, are addressed elsewhere (Sarasin and Sommer 2010). The present chapter aims, first, to define the target audiences of paleoanthropological reconstructions and their specific goals, perceptions, and techniques, and then, by way of a concrete case study, to follow the change of Neanderthal reconstructions from a historical perspective. Finally, the implementation of certain very recent imaging techniques and shape analysis methods in this field will be discussed.

Methods of Facial Reconstruction

Craniofacial reconstruction (CFR) techniques have developed intensively during the last decades and led to a wide field of research and application. In the context of forensic analyses, special quality requirements have to be fulfilled in order for facial reconstructions to serve the aim of identification and allow for reproducibility of results. The variety of techniques used in the reconstruction process, as well as the different forms of presentation, differ from each other in how they address these requirements of the forensic recognition process. The development of computerized methods in recent years has helped to objectify facial reconstructions and to reduce artistic interpretation, rendering these innovations of special importance to forensic work.

In contrast, early hominid reconstructions have a choice between depicting a species type and capturing an individualized appearance. Research has focused on implementing automated procedures and improving our knowledge about the correlation of bone and soft tissue, which helps in generating realistic facial surfaces (Wittwer-Backofen 2012). While this work addresses the requirements of forensic anthropology (Stephan 2009), it is less helpful in paleoanthropology, where there is no reference for soft tissue thickness and shape.

Principal Criteria of Craniofacial Reconstruction

For the reconstruction of a facial surface, including elements like eyes, nose, or mouth, precise knowledge of the interdependence of skull shape and facial elements is essential. This includes, for example, knowledge of the proper localization of the eyeballs, their size and protrusion, or of mouth width as estimated from inter-canine distances in modern humans (Stephan and Murphy 2008). Whereas such correlations and their variability may be studied fairly well in sample populations of living individuals, no direct control mechanism is available for work on human ancestors which are represented by fossilized hard tissue materials alone, except for very few existing brain casts.

A second precondition is knowledge of the thickness of the soft tissue layer to be modeled onto the skull. Based on modern human samples, this derives a surface prediction of the face. However, several errors may occur in this step: as facial soft tissue depth has been studied for a limited number of facial landmarks only, interjacent areas are modeled as mere approximations, depending on the scientist's experience or the artistic skill of the practitioner. Apart from the limitation to specific available landmarks, published soft tissue data often suffer from small reference samples, unsuitable techniques, or insufficient background data for specification of soft tissue thickness according to age or sex (Helmer 1998; 34 landmarks). Even less information is available on ethnicity or nutritional status (De Greef et al. 2006; 31 landmarks). In the future, studies drawing on digital 3D imaging, such as computed tomography, may generate more adequately sized datasets from clinical patients, once the issue of position-dependent soft tissue shift is resolved (Claes et al. 2006a; Starbuck and Ward 2007; Wittwer-Backofen et al. 2007). These requirements are also not satisfied in the case of reconstructions of human ancestors, due to the obvious lack of reference samples.

A third limitation in the reconstruction process of modern humans relates to the textural details of the face, which are not directly linked to facial bone surface traits but instead inferred from additional information, such as ancestry or specific living conditions. Examples of such textural characteristics are pigmentation, wrinkles, and hair style.

Attempts to overcome these limitations when reconstructing premodern hominids draw on comparisons with our closest relatives in order to infer the appearance of our ancestors. In the past, this practice was only weakly supported by scientific facts. Just recently, molecular genetics has started to contribute a new element to the debate by studying, e.g., the evolution of skin color and of body hair (McEvoy et al. 2006; Rogers et al. 2004) based on data from extant populations (the HapMap project) and supported by hypotheses on evolutionary mechanisms of adaptation (Jablonski and Chaplin 2000; Jablonski 2004). For now, however, we have few clues, leaving us with a very incomplete picture.

Skull Bone Reconstruction

A basic factor for the prospects of a craniofacial reconstruction is the state of preservation of the skull. Ideally, the skull should be completely preserved, with its shape intact and not deformed or fragmented by postmortem diagenetic conditions, such as mechanical soil pressure or exposition to the surface.

Paleoanthropological fossils that meet these requirements are rare. Most of them are heavily distorted and fragmented. Repositioning and completion reconstructions represent interpretations which are often controversial. This mainly applies to older finds that were object to mechanical invasion, requiring assembly of fragments with missing joints. Recently, a set of primarily computer-based methods for the reconstruction of skulls has become available (Zollikofer and Ponce de Léon 2005; for an overview see Uhlhaas 2007). Digital representations of bone fragments from computed tomography can be fused in a virtual 3D environment, in the process allowing for the correction of deformations. Where parts of paired bones are only available for one side of a specimen, these can be mirrored and inserted virtually, assuming lateral symmetry. Missing parts, such as mandibles, can be reconstructed with a certain probability through size adaption of mean shapes. This has been shown for reconstructions in modern humans and can also be applied in paleoanthropology, if comparable data of the same taxon are available (Schlager et al. 2011).

Manual Techniques

The first attempts to reconstruct faces from skulls were made at the end of the nineteenth century. The aim was to recreate the faces of famous persons, such as Johann Sebastian Bach (His 1895) or Friedrich Schiller (Welcker 1883). It is worth mentioning that the basic procedures of manual 3D reconstruction techniques that are still in use today were established and discussed in the 1920s already. For example, Von Eickstedt (1925) discusses the advantages and disadvantages of modeling soft-tissue surface in bulk, only restricted by soft-tissue markers, compared to the detailed modeling of facial muscles based on accurate anatomical knowledge.

One of the central characters in the history of scientific facial reconstruction was the Russian anthropologist Mikhail Gerasimov, who in the 1930s successfully applied his profound knowledge concerning individual skull traits and their correlation to soft tissue, thereby starting a new era of CFR based on plastic modeling (Gerasimov 1968). Gerasimov amassed volumes of empirical data that were left almost undocumented. Besides forensic cases and reconstructions of historical personalities such as Schiller, his research interest focused on paleoanthropological reconstructions. His own reconstructions, which became classics, include the *Homo erectus* specimen from Choukoutien, the Steinheim skull (interpolating the missing mandible), the Neanderthal man from La Chapelle-aux-Saints, the Broken Hill (today Kabwe) skull, and the Late Paleolithic Cro-Magnon man.

Gerasimov used skull casts (today replaced by 3D prints) as the basis for his sculptures. In a first layer, facial muscles are modeled in clay, plastiline, or wax according to muscle attachment markers and bone shape. After the eyeballs (formerly clay models, today often glass eyes) have been inserted into the eye sockets, the final skin surface is modeled by connecting the surface markers and giving the face its individual appearance (Gerasimov 1968).

The principles of Gerasimov's method have been widely applied, though precise reproducibility and application of his method was made impossible by shortcomings in his publications (Ullrich and Stephan 2011). The method became known as the “Russian method” and was further developed into the so-called “Manchester method” (Prag and Neave 1997). Another, later modification has been taken up mainly among American forensic anthropologists. This so-called “American method” consists in modeling a single soft tissue layer (Taylor 2001). Reconstruction is performed much faster and with less effort, but the method is less suitable to implementation of variable, individual skull traits.

Artistic refinements such as single hair insertion and detailed texture modeling are technically possible and used for museum presentations. Specialists working on paleoanthropological reconstructions – such as Elisabeth Daynès in France, John Gurche in the United States, or Alfons and Adrie Kennis in the Netherlands – predominantly are referred to, and refer to themselves, as artists rather than scientists. They claim to be supervised by paleoanthropologists, however. During the last decades, elaborate 3D plaster techniques have gained in importance in the visualization of early hominids because these artistic approaches focus on individualized faces with specific texture information (Taylor 2001; Wilkinson 2010). In museum presentations of historical persons or fossil hominids, for example, this type of facial reconstruction has been an impressive success because of the emotions and empathy it evokes (Berge and Daynès 2001; Gurche 2013). However, little information about the underlying rationales regarding soft tissue thickness or placement of facial elements is published by this group of specialists, thus supporting the impression of a predominantly artistic approach.

In short, the clay modeling techniques that were the most commonly applied methods in the early days of facial reconstructions, still play a significant role and are being further developed now into elaborate sculpture techniques for reconstruction of early hominids. In forensic contexts, however, craniofacial reconstructions are increasingly replaced by virtual methods.

Computer-Based Craniofacial Reconstruction

Most scientific approaches to CFR deal with a very technical aspect of soft tissue reconstructions, namely, the individual variability of soft tissue thickness. They are usually directed towards a standardization of the process. This is indeed an important part of the reconstruction challenge, associated with many unsolved questions and unmet desiderata, which among specialists is leading to a growing interest in 3D form analysis (Claes et al. 2010; Wilkinson 2005; Vignal and Schuliar 2002).

Recent developments in digital imaging techniques, such as surface scanning, CT, and MRT scanning, have made it possible to acquire large databases of 3D representations of human heads. Though a digital image is never an exact copy, it still provides very detailed information about the structures represented. During the last two decades, CFR researchers have been trying to exploit these sources of information. In this section, we will provide a short survey of ways to generate algorithms that estimate the skin surface from information on the underlying bone formation. Only those methods that use semi-automated processes are taken into account here, leaving aside those that employ computer graphics to emulate manual reconstruction (Wilkinson 2010).

The basic workflow in computer-assisted CFR is very similar across the various approaches: after examination of the skeletal remains, a template of the soft tissue has to be adapted to the shape of the skull. The prerequisites needed for most approaches are (i) a database containing both bone and skin information (early studies restricted to a single configuration), and (ii) a mapping algorithm applying the information from the database onto the skull. The computer-driven approaches are to some extent a copy of the manual methods, except that they replace the individual knowledge and skill of specialists with information from a database. In doing so, they gain independence from any particular artist/scientist performing the reconstruction. On the other hand, computer-assisted CFR can only be as good as its database and underlying algorithms.

In general, the prediction is performed by using a soft-tissue representation generated from the database and applying a deformation based on a connection between skin and skull surfaces provided by the database. An extensive survey of computer-based reconstruction approaches can be found in Claes et al. (2010).

Survey of Contemporary Methods

Due to the novelty of the imaging techniques which allow to acquire digital 3D representations of skull and skin tissue, computer-assisted methods do not reach back in time as far as manual CFR methods. Vanezis et al. (1989) were the first to propose a reconstruction method based on digitized skulls. Basically, it mimics the “American method” (see above) using 3D representations of the dry skull, where virtual soft-tissue thickness dowels are being placed and the surface between them interpolated. This basic workflow has been followed by most researchers since. The main differences between protocols fall into two types: first, the way the information about the skull is represented, and second, the way the information from the database is transferred onto the skull of the specimen whose facial appearance is to be reconstructed. The following list notes these differences and cites the corresponding literature:

Differing types of skull representation (Fig. 1)

- Sparse sets of landmarks or virtual tissue dowels (Evenhouse et al. 1992; Vanezis and Trujillo 1996; Vanezis and Vanezis 2000; Claes et al. 2006a, b)
- Dense sets of feature points (Jones 2001; Paysan et al. 2009)
- Crest lines on the skull, consisting of discrete 3D coordinates (Quatrehomme et al. 1997; Subsol 2002; Subsol and Quatrehomme 2005; Turner et al. 2005, 2006)

Differing methods of template selection/generation

- A single reference mapped onto the target skull (Evenhouse et al. 1992; Vanezis and Trujillo 1996; Vanezis and Vanezis 2000; Subsol and Quatrehomme 2005; Pei et al. 2008)
- A reference derived from multiple database entries (Vandermeulen et al. 2005, 2006; Claes et al. 2006a, b; Paysan et al. 2009)

Fig. 1 Different types of skull representation. Methods: *left*: sparse set of landmarks; *center*: dense feature points; *right*: crestlines on a skull representing the surface's curvature

All of these variants share the fact that information about the complete skull as well as skin information is used for mapping a template face onto a dry skull.

Problems Arising in the Reconstruction of Extinct Hominid Species

The problems that occur when trying to apply the above methods to bone material of extinct hominid species are obvious: the central feature of semi-automated methods is an extensive database from which the estimation algorithms are derived – the database that serves to "teach" computer programs the association between bone structure and the covering facial surface shape. For extinct species there is no way to acquire a priori information about this association. When automated methods are used on non-*sapiens* bone material, the result will be a face from *H. sapiens* deformed onto the skull of another species. Even when regularization is applied in order to increase the probability of the estimation, the reconstructed face will basically be a distorted face of a modern human. In his dissertation, Claes (2007) takes this approach to a Neanderthal skull; the result appears to resemble a human face turned into a grimace fitting the Neanderthal skull, rather than the face of another hominid species.

Since computer-based algorithms rely on machine-learned correlations drawn from existing datasets, these approaches are of limited applicability to hominid reconstructions; for obvious reasons, data from the specific taxon are not available. All such approaches, when applying data from *H. sapiens*, will lead to a strong bias in soft tissue reconstruction towards modern humans.

Target Audiences of Paleoanthropological Reconstructions

Ever since the general acceptance – both in science and in public opinion – of Darwin's theory of evolution and the subsequent paradigm shift, which demoted humans from being the crown of creation to being just another species that evolved from previous forms, artists and scientists have been trying to visualize our ancestors. It is fruitful for the interpretation of these reconstructions to analyze the context within which they were produced: interpretations of paleo-/prehistoric findings are often entangled with ethnocentric preconceptions and are used implicitly or explicitly to support these preconceptions. A recent example of this entanglement is the case of the so-called Kennewick Man, involving an approximately 9,400-year-old skeleton found in Kennewick, Washington. In the absence of thorough scientific analyses, public media and various groups – among them a neo-pagan Norse cult – tried to exploit the acclaimed Caucasoid skull features of this skeleton to create bizarre theories about a prehistoric American of European descent.

Before we concern ourselves with the historical and scientific implications associated with paleoanthropological reconstructions, we will briefly discuss their intended target audiences. Generally speaking, there are two main target groups: (i) the scientific community of paleontologists and paleoanthropologists and (ii) the general public. In the process of considering these groups, we will no differentially cover the wide variety of hominid reconstruction techniques in play, from rough drawings to highly detailed dermoplastics. What matters in the present context is that all of these techniques go beyond pure documentation of fossil remains.

The Scientific Community

At first glance, visual reconstructions of extinct hominids might be considered irrelevant in the field of anthropology, because their contribution to scientific insight is marginal. Most details of visualizations, such as facial expression or life environment, are only loosely related to hard facts. As mentioned above, scientific publications tend to concentrate on scientific argumentation and quantitative analyses, only occasionally adding facial or whole body reconstructions to the text.

It would be a mistake, however, to deny any effect of reconstructions on scientific theories. These depictions are "not just visual translations of theories about past humans" (Moser 1992, p. 831) but play an important role in shaping or even creating the sociocultural background for the propagated theories. Reconstructions can be understood as hypotheses rather than illustrations (Drell 2000; Sommer 2006; Stoczkowski 2002), exploiting the power of visual language to make their point. Despite the fact that these visualizations are usually presented in newspapers, magazines, or museums conceived for a wider public, they still are able to influence the scientific community by manipulating public opinion and creating biases towards specific theories. Thus, they are fighting the same war for expert favor on a different battlefield. As will be seen below (see section "The History of Neanderthal Depictions: Between "Us" and "Them""), it can be argued that reconstructions played a crucial role in the basic understanding and definition of Neanderthals at the beginning of the twentieth century, when two diverging theories of human evolution (the multilinear vs. the unilinear view; cf. Moser 1992) both employed powerful images. Science and its results are always, at least to some extent, a product of specific social and cultural circumstances and deeply rooted within this social context. Therefore, effective control and manipulation of this social context may be essential to a theory's success, not only in the public opinion but also within the scientific community and, to a considerable degree, in the business world supporting science. Although they are not the main target audience for hominid reconstructions, scientists and their respective theories are likely to be affected by popular visualizations of human ancestors, through their integration into a common cultural environment.

Nonscientific Audiences

The field of paleoanthropology is of great interest to the general public because it deals with human evolution and hence plays a fundamental role in human self-definition and self-understanding (Trinkaus and Shipman 1993a, b). When, after the general acceptance of Darwin's theory, (Western) human self-definition and self-esteem could no longer be based on the belief that humans were the most valuable product of a divine creator, placed into a world that was centered around their needs, people needed to get accustomed to the idea of being one species among many and subject to the same biological principles as others – such as natural selection and evolution. Scientific results from the field of paleoanthropology, therefore, were deemed to be of high public interest. As an example of this evident hunger for information, one might mention the outrage of socialist media in France about the relatively high price of Marcellin Boule's 1913 monograph on the Old Man of La Chapelle-aux-Saints, which made the book unaffordable for the working class (Sommer 2006). However, scientific research reports are often hard to read for nonscientists, and the meaning and implications of the reported results can be far from intuitive. For this reason, visualizations became an essential tool for introducing theories of human evolution to the public (Sommer 2006). It is important to note here that visualizations never merely serve illustrative purposes but also, always, function as a vehicle for specific theories (Hamilton 2011). Today, just as in the last century, public access to these visualizations occurs mainly through mass media, such as television or magazines, and through public display in museums.

Museums

Museums aim both to educate and to entertain their visitors. Yet unadorned exhibitions of fossilized hard tissue remains of early hominids do not hold much interest for the average visitor: fragmented and fossilized bones bear only little visual resemblance to the specimen during its lifetime, and the non-expert public will likely find it hard to grasp the meaning and implications associated with a specific find. Also, time spent on a museum visit is limited, as is visitors' attention span. Dioramas or a body and facial reconstruction are helpful, therefore, insofar as they can convey a lot of information without demanding extensive text reading. Additionally, spectacular visualizations can generate a lot of welcome publicity, increasing visitor numbers and generating much-needed museum revenue. The most impressive reconstructions of extinct hominids are therefore commonly part of elaborate museum dioramas with fully physical, life-size elements, supporting the impression of a realism and thus implicitly proclaiming the truth of the theories underlying the design of the depicted scene. These visualizations are more or less dissociated from their causal explanations and their contextualization within a theoretical framework – that is, from much that would be essential for scientific understanding. This may lead to the integration of reconstructions into pre-existing pre- and misconceptions about human evolution, rather than explaining the current scientific models (Scott 2010).

Public Media

Public media – be it television, print media, or internet-based services – are using similar methods as museums: they distill complex theories down into brief (spoken or printed) texts accompanied by visual transcodings. Making the content easier to understand and more attractive to potential audiences demands radically simplified expositions of underlying theories, illustrated with suggestive images that rather serve to support preconceptions than to present actual research results. Another obvious problem is the fact that many media science writers are not scientists themselves, leading to distortions due to wrongly interpreted research results (Sommer 2006). There also seems to be an urgent need to accompany any news about current research on human evolution with images of reconstructions of extinct hominids. A recent example can be found on *Spiegel Online* (http://www.spiegel.de/wissenschaft/mensch/falsche-altersbestimmung-neandertaler-verschwand-frueher-als-gedacht-a-881640.html [Version from: 08/02/1913]), the online presence of a major German magazine, where information about new dating results of Neanderthal fossils is illustrated with a large image of a dermoplastic reconstruction of a Neanderthal – completely irrelevant to the text. The image merely serves as an eye-catcher, giving the reader something tangible to relate to. The original journal article cited by *Spiegel* (Wood et al. 2013) contains, of course, no such visualizations but instead presents raw data in table form and discusses interpretations; the only visual elements are maps and drawings of a specific archaeological site.

The History of Neanderthal Depictions: Between "Us" and "Them"

Soft-tissue reconstructions of extinct hominids intend to associate dry fossilized bones with the appearance the individual might have had during his or her lifetime. Since soft tissue decomposes completely after death, little evidence exists on the relationship between lifetime appearance and remaining material in extinct species (see section "Methods of Facial Reconstruction"). Visualizations therefore are necessarily subject to influences independent of the actual physical remains. Such influences might cover sociocultural bias and/or the artists'/scientists' individual preconceptions and may result in erroneous conclusions concerning the correlation between bones and soft tissue shape and texture. Especially *Homo neanderthalensis*, our most closely related hominid species both temporally and phylogenetically, has undergone multiple shifts in reception paradigms since the first finding (first in being recognized as an extinct hominid species) in 1856 in the Feldhofer Cave. The semantic range of these receptions can be summed up in the dichotomy of "*the same*" versus "*the other*," where the latter stands for a view in which close hominid relatives of man serve as the "outside" that defines the borders of humanity. From conceptions of an apish brute to ones of a relative who is only slightly different from us, all nuances have been covered by Neanderthal reconstructions based on the same physical objects: fossil bones.

Evaluations of scientific research in paleoanthropology as a field of physical anthropology are mainly performed in the social sciences, e.g., in sociology and archaeology. These follow their own scientific traditions and employ their own terminology and modes of argumentation. Besides the reconstructions themselves, the resulting insights constitute an important element in the interpretation of hominid reconstructions. Therefore, this chapter presents concepts from these fields of social science in their original terminology, in keeping with common practice in the paleoanthropological literature.

The intense focus on *H. neanderthalensis* is, of course, owed to the large number of available fossils, as well as to the fact that Neanderthals were the first species to be identified as an extinct hominid species. This makes the Neanderthals a perfect case study for inquiry into reciprocal interactions between sociocultural environments loaded with intrinsic preconceptions, individual points of views regarding the scientific interpretations of fossil remains, and the resulting multitude of divergent reconstructions of extinct hominid species. Indeed, the topic has been discussed intensively for the last 20 years. In this section we offer a survey of the central arguments and the changes in paradigm associated with different eras of reconstruction (see Table 1).

The Nineteenth Century: Early (Pre-)conceptions

When the fossils of the type skeleton of *H. neanderthalensis* were found in the Feldhofer Cave in 1865, the local schoolteacher Johann Carl Fuhlrott postulated that they belonged to a human that had lived during the last Ice Age. The temporal proximity of this finding to Charles Darwin's publication of *On the Origin of Species by Means of Natural Selection* in 1859 made it a perfect example for man's redefinition as "just" another species, subject to natural selection and evolutionary processes (Drell 2000). Auffermann and Weniger (2006) as well as Trinkaus and Shipman (1993a) claim that the Neanderthals gained their initial public and scientific image from the European archetype of the "savage man". This image was applied to the Neanderthal, who served as "crown witness" (Auffermann and Weniger 2006) for the theory of evolution that was to replace the religious view of man as the major achievement of a divine creator. Thus, the first reconstructions were applications of this archetype rather than scientifically sound approximations of the Neanderthals' actual physique.

Table 1 Timetable of Neanderthal reconstructions, listing scientific paradigm and scientific changes, influential in the specific period

Timeframe	Scientist/artist (selection)	(Scientific) paradigm of appearance	Scientific changes
1856–1909	Illustration in *Harper's Weekly*	Neanderthals as incorporation of the "savage man"	Darwin's *On the Origin of Species*
	Mouston, Friedenthal, Schaafhausen		
1909	Boule	Stooped, bent-legged, apish	Complete post-cranial skeletons (La Chapelle-aux-Saints, La Ferrassie)
1911	Keith	Modern, sensitive, wearing body decoration, manufacturing tools	
1913	Boule	The facial reconstruction is restricted to muscle tissue. The neck appears to refer to the vertebral pathologies	
1915–1918	McGregor/ Osborne	Humane appearance	
1920s	von Eickstedt, Blaschke, Weinert, Mollison	Heavily relying on Boule's paradigm. Neanderthals are suggested to be dim-witted sub-humans	
1930s	Gerasimov	Gerasimov's reconstruction is relatively human-like	Findings of more ancient hominid species (*H. erectus*, Australopithecines)
	Coon (based on the reconstruction by McGregor)	Coon indicates that dressed modern, the Neanderthal is indistinguishable from modern humans	
1950s–1980s	Gerhard Wandel, Jay Matternes/Eric Trinkaus	Neanderthals are similar to modern humans, both in appearance and behavior. "Modern spirits trapped in archaic bodies"	Confutation of Boule's analyses by Patté, Arambourg, Straus and Cave (1955–57)
			Findings in the Guattari Cave, leading to the (false) postulation of ritual cannibalism.
			"Flower burial" and social behavior deducted from findings in Shanidar Cave (1971–75)
1990s – now	John Gurche, Elisabeth Daynés, A&A Kennis	Depiction of Neanderthals as humane but distinct species. Capable of cultural achievements and human emotions	Neanderthal genome project

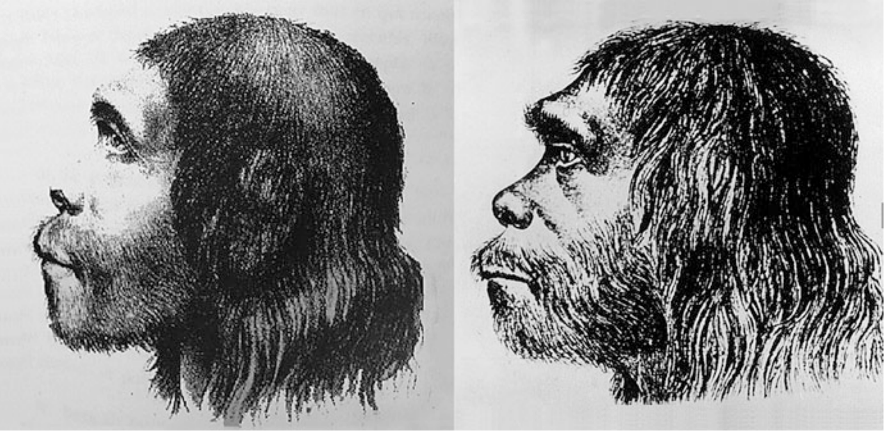

Fig. 2 Reconstruction by Schaaffhausen based on the skeleton from the Feldhofer Grotto. *Left*: Initial version from 1876; *right*: revised version from 1888

The probably first visualization of a Neanderthal was published in the magazine *Harper's Weekly* (Weltersbach 2007). It depicted a ready-to-fight male at the opening of his cave, accompanied by a dog. In the nineteenth century, evolution was often understood as a process of improvement, both physically and morally, from the more primitive to the more complex. The most advanced state was, of course, that of Western civilization, with other human societies placed below. Prehistoric life thus could be approximated by tracing the evolutionary slope "downward." The resulting body visualizations express these preconceptions without being supported by evidence from fossil bones. Other popular visualizations from this period are a romantic lithograph by Mouston (1887) (cf. Henke et al. 1996; Schrenk and Müller 2005), a drawing of a "cave dwelling Neanderthal" (Drell 2000) by Friedenthal, and two reconstructions by Schaaffhausen – the original version from 1877 depicts a mild-looking young man, whereas its revision from 1888 appears more brutish and simian (Fig. 2). Schaaffhausen's reconstructions differ from the visualizations of his contemporaries insofar as he worked closely with the skull bone, which, however, lacked any facial parts.

Boule vs. Keith: A Struggle of Views

When the geologist and paleontologist Marcellin Boule examined the remains of the Old Man from La Chapelle-aux-Saints in 1908, in which (unlike the Neanderthal skeleton from the Feldhofer Cave) facial bones were preserved, he created a stereotype that stuck to the Neanderthal throughout the first half of the twentieth century: that of a species of stooped, apish appearance, too primitive to be a direct ancestor of modern humans. Boule's views were mainly based on a faulty analysis of vertebral deformations, caused by osteoarthritis, which led him to the erroneous conclusion that the entire *species* (and not only this particular individual) lacked a spinal column suitable for completely upright posture. Some authors argue that Boule's neglect of the pathological nature of the vertebral shape was "fully cognizant" (Trinkaus and Shipman 1993a, p. 196), in order to fit the results of his analysis to his theory of human evolution: Boule was convinced that human evolution was to be understood as multilinear, forming a phylogenetic tree with dead ends. A detailed analysis of the motivations that drove Boule to his conclusions can be found in Hammond (1982).

Boule's theory stood in opposition to the common unilinear view, shared by influential contemporary scientists like Gustav Schwalbe and Dragutin Gorjanović-Kramberger (Henke 2006), who postulated a single line leading directly from earlier hominids to modern humans. At the beginning of the twentieth century, there was indeed no physical evidence available to support Boule's theory. A hominid species temporally not very distant from modern humans, yet exhibiting apish traits, would have well proven his point. Boule reported his conclusions concerning Neanderthal appearance to the French Academy of Sciences between December 1908 and June 1909, stating that most parts of the skeleton showed simian-like characteristics, while neglecting to point out a multitude of traits shared with modern humans.

The first reconstruction based on Boule's analyses was the influential drawing by the Czech artist František Kupka depicting the Neanderthal as a brutish ape, lurking ready-to-fight behind a rock with a boulder in one hand and a club in the other. The artist was completely ignorant of the large number of elaborate tools associated with the Mousterian culture that were already known at that point. The Neanderthal's body is covered with hair, and his facial expression is grim and lacks human features. The image was published in February 1909 in the French Magazine *L'Illustration* and 1 week later in the English magazine *London Illustrated News* (Moser 1992). It gained its importance from the claim to be not just hypothetical or based on the imagination but to be "*accurate*" (Reichart 1909). Moser (1992) states that this claim transformed its meaning from being an illustrative figure accompanying text to being a "scientific document" itself. By attesting accuracy, the image purports to incorporate scientific research results directly.

While it is difficult to estimate precisely the extent of Boule's influence on Kupka's rendition of the Neanderthal's body itself, it is known that he instructed the artist about details of the landscape (Reichart 1909; Moser 1992; Sommer 2006). Moser (1992) concludes that the fact that Boule allowed the image to be printed and associated with his name and research makes it safe to assume that he generally agreed with its content. When Boule finalized his analyses, published in the *Annales de Paléontologie* (Boule 1911, 1912, 1913), the stooped posture shown in the image, resulting from the (pathologically deformed) vertebral shape, served as a central argument that Neanderthals were an extinct side branch of human evolution – and therefore not our direct predecessors. To emphasize his point, Boule depicted the proposed Neanderthal posture from the Old-Man of La Chapelle-aux-Saints next to the skeleton of an Australian Aborigine; these native

Australians were, at that time, believed to be the most primitive of modern humans. The gist of the comparison is obvious: if the most primitive of living men are already that distant from Neanderthals, how can modern humanity have evolved from Neanderthals in such a short period of time? One might conjecture that, at the least, Kupka's powerful visualization influenced Boule's subsequent theoretical conclusions (Moser 1992).

Two years after Kupka's image of the brutish Neanderthal was published, Amédée Forestier, in collaboration with the anthropologist Arthur Keith, produced a reconstruction drawing which diametrically opposed Boule's/Kupka's view in the very same British magazine, the *London Illustrated News* (Keith 1911). The image depicts a male individual sitting in a homely cave by a fire, manufacturing tools from flint stone. He wears fur and a necklace. By choosing this set of accessories, Keith assigns fundamental insignias of human civilization to the Neanderthals: control of fire, production of tools, clothing and body decoration. The male figure also wears his hair braided and woven around his head. His gaze is not apish at all but shows sensitivity and diligence. The image clearly indicates that the Neanderthal is rather "the same" as we are, and not too different at all. This assemblage was of course not based on scientific analyses but tried to enforce and emphasize, once again, theoretical constructions and beliefs of its creator (Moser 1992; Weltersbach 2007). At that time, Keith, unlike Boule, was convinced that humanity had evolved in a single line of descent from earlier species, without dead ends. Ultimately, however, Boule's point of view prevailed, not least because Keith changed his opinion radically only 1 year after the publication of the article in the *London Illustrated News*, now taking up Boule's position. As Moser (1992) points out, Keith's new perspective was again expressed in a visualization, where Keith now uses the same features that Kupka/Boule assigned to their Neanderthal: those of "stooped, club-wielding brutes."

The Aftermath: An Image That Sticks

The prevailing image of the Neanderthal, drawn by Kupka/Boule, enforced the scientific conclusions concerning the Old Man of La Chapelle-aux-Saints. As a visualization of mainstream theory, it was widely accepted in the first half of the twentieth century, thus "setting the cornerstone of Neanderthal reception" (Auffermann and Weniger 2006). Most reconstruction attempts of Neanderthals during that period referred to Boule's analyses to justify their approach. Consequently, Neanderthals appear either as stooped, apish brutes or as dim-witted, degenerate humanoids that serve well to make modern humans appear noble and intelligent. One might view this as an attempt to rehabilitate humankind to its pre-Darwinian position as the crown of living organisms – this time not owing to divine creation but to its superior evolutionary status when compared to other, "inferior" hominids. A very extensive display of *H. neanderthalensis* as human's dim-witted cousin can, for example, be found in the reconstructions by Frederick

Blaschke, which accompanied the book *Neanderthal* (*Mousterian*) *Man* (Farrington and Field 1929): all his depictions of Neanderthals suggested the species to be lost in a hostile environment, incapable of surviving on its own. Von Eickstedt (1925) published an elaborate article describing minutely the steps taken to reconstruct the facial surface of the Old Man of La Chapelle-aux-Saints, in which he justified soft-tissue depth and appearance by citing Boule's monograph and emphasizing the apish and primitive nature of the species (e.g., by referring to the "chimpanzoid vertebrae"). As a result, exactly this preconception is reproduced in a modeled bust exhibiting simian traits such as massive supra-orbital rims; the latter seem to be over-exaggerated in light of the supraorbital bone structures.

A few exceptions to this mainstream paradigm for reconstructions do exist: a bust created in 1915 by the artist Howard McGregor, guided by the American paleontologist Henry Fairfield Osborne, depicts a Neanderthal that appears intelligent and sensitive, and not that different in appearance from modern humans (Auffermann and Weniger 2006). Interestingly, one of the least suggestive reconstructions is by Boule himself (Fig. 3). It only shows facial muscles, without added skin layer, texture, or further accessories. This bust actually limits itself to details of anatomical features which can be scientifically justified, without supplying additional information inspired by preconceptions and the imagination.

Fig. 3 Bust of the Old Man of La Chapelle-aux-Saints under guidance of Marcellin Boule

Coming Closer

A shift in the Neanderthal's image was slowly introduced in the 1930s, triggered by a variety of scientific and cultural changes. During the 1920s and 1930s new fossils of previously unknown, extinct hominid species, the Australopithecines, were discovered in Africa. At this point the emerging variety of *pre-sapiens* hominid species made it increasingly difficult to maintain a simplistic view of human evolution. Meanwhile, *H. neanderthalensis* appeared more and more similar to modern humans, especially when compared the older hominids (Trinkaus and Shipman 1993a). Boule's conclusions regarding stature were first questioned by the German Kleinschmidt in 1938. However, the final dismissal had to wait until the mid-1950s, when different scientists (Patté, Arambourg, Straus and Cave) concluded almost independently that the vertebral shape of the Old Man of La Chapelle-aux-Saints was actually owed to osteoarthritis rather than indicating a species-wide trait that would have led to a forward-bent stature (Trinkaus and Shipman 1993a). The most powerful visualization indicating this change in paradigm is the famous drawing presented by Carlton Coon (1939), depicting the Neanderthal reconstruction by McGregor (see above) now shaved, dressed in contemporary clothing, and wearing a hat. The image's caption states: "Although we do not know that the reconstruction of the soft parts is accurate, nevertheless the facial features were probably essentially human" (Coon 1939, p. 24). This exemplifies the radical shift from the Neanderthals being perceived as "the other" to being "similar." The simian-like appearance, closer to a beast, has turned into a species that would not be recognized as different from humans when put into our modern sociocultural context and equipped with suitable requisites.

Another reconstruction from this period that also makes the Neanderthal appear more human is a bust from 1938 created by the famous Russian anthropologist Michail Gerasimov. It is again based on the skull of the Old Man of La Chapelle-aux-Saints and has an apparently human facial expression, although it is covered with a wild mop of hair (Gerasimov 1949). Aside from becoming more human, this Neanderthal has lost his "brute benightedness" (Trinkaus and Shipman 1993a), not least due to Alberto Blanc's erroneous postulation of *ritual* cannibalism among Neanderthals. While there had already been conjectures about habitual cannibalism among Neanderthals, based on the findings from Krapina, Croatia, this time the relevant clues were associated with sophisticated burial rites. Blanc based his claims on findings from the Guattari Cave in Italy, which he failed to identify as a hyena den, instead interpreting the traces of animal teeth on the surface of hominid bones in it as the results of burial rites involving defleshing and consumption of the deceased's remains (White et al. 1991; Trinkaus and Shipman 1993a).

Despite progressive achievements in science and the resulting change in Neanderthal reception, Boule's primitive image still prevailed in popular Neanderthal depictions until the 1960s. For example, artists like Zdeněk Burian or Charles Robert Knight influenced the public image by producing reconstructions to illustrate books or accompany museum exhibitions where Neanderthals were visualized according to Boule's analyses and/or the associated drawing by Kupka (Auffermann and Weniger 2006).

Flower People

Another potential connection between scientific theory and scientists' sociocultural environment can be seen in the interpretation of the fossils from the Shanidar Cave in Iraq. Between 1957 and 1960, nine adult Neanderthal individuals and one child were found, four of them apparently killed by rockfall, the other five seemingly buried intentionally. Soil samples from the immediate vicinity of Shanidar IV contained a large amount of wildflower pollen. Solecki (1971) interpreted this as evidence for a sophisticated burial ceremony, involving large amounts of flowers. The subsequent monograph about his research was titled *Shanidar*: *The first flower people*; it fit neatly into the general sociocultural context of the late 1960s and early 1970s. Burial rites which seemed to be similar to our own made it easier to accept Neanderthals as close relatives. Thus Solecki (1975, p. 880) writes: "The discovery of pollen clusters of different kinds of flowers [. . .] furthers our acceptance of the Neanderthals in our line of evolution." He further states that this indicates that the Neanderthal "had 'soul'". More recent evaluations doubt these interpretations and suggest alternative causes for the accumulation of flower pollen, for example, that they had been carried in by rodents (Sommer 1999). Another important – and undisputed – finding from Shanidar, however, is the fact that Neanderthals seem to have cared for their handicapped. Shanidar I shows signs of severe skull trauma, leaving him probably half-blind, combined with a multitude of healed postcranial bone fractures, and with an unusable right arm. As the fractures were not fatal but had healed instead, his group members must have taken care of him, providing food and assistance so that he could master his everyday life. These inferred acts of mercy and *humanity*[*!*] made the Neanderthals more presentable as close relatives with whom we share similar moral standards. Solecki subsumed this impression under the extremely simplifying formula of the Neanderthals having a modern spirit trapped in an archaic body (Solecki 1975). He prompted a shift in the argumentation from mere interpretation of skeletal remains to conclusions concerning the Neanderthals' *behavior* (Trinkaus and Shipman 1993b).

Many reconstructions from this period depict the Neanderthals as human, with an appearance almost indistinguishable from that of modern humans; examples are the "squatting Neanderthal" by Gerhard Wandel from 1962 and the reconstructions by Jay Matternes, depicted in Henke et al. (1996).

Readjusting the View

Recent studies have led to a more refined picture of Neanderthals as hominids very similar to modern humans yet distinct in their morphology. Their differing morphological features were most likely adaptations to the environment of Upper

Paleolithic western Europe. While some of these features are very distinct from those of modern humans, many others are not. Additionally, advances in scientific methods, such as genetic sequencing of ancient DNA, have contributed greatly to our understanding of the phylogenetic relation between modern humans and Neanderthals. Studies have proved genetic differences to be relatively small. Indeed, there likely was some interbreeding with early European *H. sapiens* (Green et al. 2010). At this point it is fair to conclude "that the humanity of Neanderthals cannot be denied anymore" (Auffermann and Weniger 2006, p. 188).

As a result, most recent reconstructions tend to visualize Neanderthals as very similar to modern humans (Henke et al. 1996; Koepfer and Gurche 2003). Many artists make use of latex-based dermoplastic that allows the creation of astonishingly lifelike appearances, giving the reconstructed specimens personality by sculpturing gestures and emotional facial expressions (cf. the reconstructions of laughing Neanderthals by Alfons and Adrie Kennis or of an Ante-Neanderthal male called "The Thinker" by Elisabeth Daynès). The resulting implications of similarity to modern humans with respect to emotions and their expression are not indisputable: recent comparative genetic analyses (Green et al. 2010) suggest genetic differences on DNA sequences associated with nerve growth and brain functions (one of them implicated in autism). The reconstructed details mentioned above are in no way supported by the available material but are subject to the artists' imagination and creativity. Here again, reconstructions of extinct hominids serve as transport vehicles for a prevailing scientific view – in this case the modern view that Neanderthals are a human species, capable of the same range of emotions as we are, distinct in morphological detail but with an overall appearance not that different from our own. Since the time of Coon's Neanderthal reconstruction it has also become common to dress reconstructions as modern humans, to emphasize the fact that they would be indistinguishable from us if we were to meet them in our own, modern world (e.g., Auffermann and Orschiedt 2006).

Conclusion and Outlook

Although various virtual techniques have arisen during the last decades, reconstruction methods today still rely more on craft skills and observer experience than on exact calculations. However, computational methods are beginning to play an important supporting role. For example, recent studies explore the combination of Geometric Morphometrics and Finite Element Analyses (O'Higgins et al. 2011; O'Higgins and Milne 2013; Bookstein 2013). Geometric Morphometrics (GMM) is an approach that quantifies the shape of complex geometrical structures based on the extrapolation of well-defined coordinates (landmarks) relevant for the structure's shape. Finite Element Analysis (FEA) is an appropriate method to analyze the mechanical properties of complex structures (Richmond et al. 2005), by partitioning their geometry into a finite number of elements. Technically, FEA is a numeric procedure to solve partial differential equation systems occurring in specific physical problems. The method relies on experimental data, e.g., from compression or tensile testing, to estimate the parameters associated with the material in question.

Since the beginning of the twenty-first century, Finite Element (FE) modeling has been applied to address biomechanical issues in anthropology by assessing functional shape characteristics of anatomical structures (e.g., Witzel and Preuschoft 2006). This approach has become a common tool in paleoanthropology for mapping morphological traits onto biomechanical properties, which, in turn, can help to formulate valid hypotheses regarding specific adaptations. To create accurate FE models from fragmented fossils, GMM can provide solutions to establish biologically valid correspondences (represented by dense sets of homologous landmarks) between the shapes of recent species and their extinct relatives. These correspondences allow the deformation of a FE model generated from recent species onto the fossil remains. The generated model can be assumed to be close to the non-existent original. As a result, it is possible to create FE models of extinct species. Additionally, the method allows correction for intra-species variation, as an initial GMM analysis of a sufficiently large sample of the extant species can help identify those specimens close enough to the sample's average to serve as suitable representatives of the species.

The following examples present a selection of paleoanthropological studies which have derived interesting results from application of FEA to fossil material.

Strait et al. (2005, 2007) investigated the biomechanical benefits of increased palatal thickness – one of the most significant synapomorphies in *Paranthropus*, assumed to be related to mastication. They used CT data to generate a model of the skull of *Macaca fascicularis* in order to conduct bone-strain experiments for validation purposes. Based on this model, muscle forces relevant to mastication were simulated by FEA. To verify their hypothesis, the authors designed a second model with increased palatal thickness. The simulated output suggested that increased palatal thickness leads to a decrease of stress in the palate. These results indicate that palatal thickness has functional consequences related to mastication, and that increased thickness might be considered an adaptation to hard food.

A more recent study applies FEA methods to estimate bite forces and the muscular forces involved, comparing the results from extant primates and extinct hominid species, such as *Australopithecus africanus* and *Paranthropus boisei* (Wroe et. al. 2010). Along these lines, analyses concerning the structural rigidity of the facial skeleton may provide insight about diet and dietary adaptations of extinct species (Strait et al. 2009, 2010, 2012).

While there are presently no approaches that directly involve FEA in hominid reconstructions, it appears that results obtained by application of these methods may provide additional details regarding specific biomechanical adaptations that are probably reflected in their muscle mass, which in turn shapes physical appearance.

Based on the above examples it can be expected that technical advances will lead to a higher degree of documentation, objectivity, and reproducibility in future reconstructions. The more scientific aspects will be incorporated into the reconstruction process, the more likely it is that reconstructions will be accepted within the scientific community.

Cross-References

- ▶ Defining the Genus *Homo*
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Neanderthals and Their Contemporaries
- ▶ Prospects and Pitfalls
- ▶ Virtual Anthropology and Biomechanics

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Prospects and Pitfalls

Jean-Jacques Hublin

Contents

Abstract

Paleoanthropology is primarily rooted in the study of fossils and the analysis of sites. Dependence on these resources leads to challenges resulting from difficulty in gaining access to scarce, precious, and sometimes overprotected materials and from issues of control over field sites. The development of virtual paleoanthropology can sometimes be a way to partially solve the first problem. However, on some occasions, the access to and utilization of numerical data has also become an issue of dispute. In parallel, recent advances in studies focusing on microstructures, isotopic composition, and paleogenetics require direct sampling of the fossils. The trend in paleoanthropology is to integrate approaches from different scientific fields, and this is especially visible in developmental sciences, genetics, and environmental studies. In the meantime, dealing with

J.-J. Hublin (✉)
Department of Human Evolution, Max-Planck-Institute for Evolutionary Anthropology, Leipzig, Germany
e-mail: hublin@eva.mpg.de

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human evolution remains a sensitive topic, subject to clear ideological and religious biases. The interest of the media and of the public in this science does not always contribute to an objective approach to the questions. Finally, among other issues, the expansion of paleoanthropological studies in developing countries must depend on a decline in its colonial image.

Introduction

In many respects, paleoanthropology is a paradoxical science. Although it addresses the oldest origins of humans, the discipline itself developed quite recently in the history of science. The first fossil hominid specimen on record, an immature Neanderthal skull, was discovered in 1830 in Engis (Belgium). However, it was not until the end of the nineteenth century that certain fossil specimens were truly accepted by the majority of the scientific community as evidence for the evolutionary process that gave birth to the human species. Although very significant discoveries occurred during the first half of the twentieth century and provided the basic framework for paleoanthropological studies, the last three decades of that century witnessed a spectacular increase in the available fossil record as well as in major advances in the knowledge of past environments and the chronological background of human evolution. Moreover, the birth of paleogenetics added a new dimension to the analysis of relationships among fossil hominid species. The current state of the discipline results not only from methodological progress but also from a major effort of field research. For the public, the media, and students, it is always a matter of amazement, and sometimes of criticism, to realize that the field of paleoanthropology is such a changing terrain. If prediction is always a difficult exercise, in science as in many other domains, it is even more challenging in this particular science, which is relatively newly born and still rapidly evolving.

Another distinctive aspect of paleoanthropology lies in the fact that the study of fossil specimens remains the core of the discipline. These are rare and precious objects. It is often emphasized that for the study of some extinct groups, the specimens are fewer than the specialists who analyze them, and sometimes the competition is harsh. After an undefined period during which they remain under the relatively rigid control of individuals or groups responsible for publishing descriptions of them, they are usually curated in museums or other institutions. While the specimens are in their possession, the curating institutions may also restrict access to the fossil specimens, emphasizing their conservation rather than their scientific study. On the one hand, there is therefore strong pressure to consult the fossil material, and on the other, growing restrictions that result from a multitude of reasons that range from the desire to maintain scientific monopoly to the legitimate policy of protecting fragile and valuable objects. In parallel, new techniques for the study of the specimens have been developed. However, while these new methods sometimes resolve issues, sometimes they generate new difficulties.

Virtual Paleoanthropology

Since the 1980s, new techniques in medical and industrial imaging have revolutionized the fields of human paleontology and physical anthropology (Wind 1984; Wind and Zonneveld 1985; Zonneveld and Wind 1985) allowing the development of what has become commonly called as "virtual paleoanthropology." The growing use of computed tomography as well as industrial imaging techniques (microtomography and laser scanners) has allowed the production of 3D images of fossil specimens. Combined with stereolithography and other techniques of 3D printing, these virtual representations have opened a number of new possibilities for the analysis of the specimens. Most notable among these are:

- Virtual extraction and reconstruction (including correction of plastic distortions) (Kalvin et al. 1992; Zollikofer et al. 1995; Ponce de León and Zollikofer 1999)
- Precise quantitative analysis of inaccessible internal structure (including tiny structures, such as middle and inner ears, bony tables, and vascular foramina) and their comparison with living references (Zonneveld et al. 1989; Hublin et al. 1996; Spoor et al. 1996)
- 3D morphometric analysis with the development of new mathematical tools (Harvati 2002)
- Modeling of ontogenetic processes, biomechanical properties, and of evolutionary changes themselves (Ponce de León and Zollikofer 2001; Mitteroecker et al. 2004; Gunz et al. 2010; Freidline et al. 2012)

Growing evidence suggests that, with increasing frequency, the anatomy of fossil hominins will be systematically studied not from the specimens themselves but from virtual representations. Principal among all the new possibilities opened by virtual paleoanthropology is the reduced need to manipulate real objects. Consequently, these techniques should be welcomed by many curators. However, they also raise new questions. One is related to the quality of the data. Until recently, the CT scanners that have been used to acquire the data were primarily those available in the medical environment. Although they evolve rapidly, machines of this type have their own limitations and are not specifically designed to explore fossilized specimens filled with dense sediments. The resolution of the 3D pictures produced in this way does not allow for the assessment of fine structures at an appropriate resolution. In recent years, large museums curating fossils, as well as research institutions, have been increasingly equipped with microCT scanners, initially designed for industrial uses, which provide high-resolution data in the order of magnitude of a micron or even under. Imagery techniques based on the use of synchrotrons such as the face contrast allow the study of microstructures otherwise inaccessible to the analysis in a nondestructive way (Tafforeau and Smith 2008).

Among the pitfalls related to the development of virtual paleoanthropology is a shift from a situation where access to the fossil specimens was difficult to a situation where access to the numerical data is even more challenging. Curators are sometimes reluctant to allow repeated acquisitions of these numerical data, while the techniques and equipment evolve rapidly. Often, the data are monopolized by those who acquired them initially, and they are hard to upgrade. In the long term, databases may develop in some institutions and on the Internet (Hublin 2013). To date, however, the development of such databases has faced insuperable difficulties. The commercialization of some of these data by the institutions concerned, or the simple trading of data between teams, will remain, for some time, the only alternative.

Another concern relates to the possibility that repeated irradiation of fossil material may alter biomolecules such as ancient DNA. Although this problem has been to date little investigated, it may in the future lead to necessary choices in priorities regarding the analysis of recent fossil material.

Into the Matter of Bone

In a somewhat opposite direction to virtual paleoanthropology, there are a number of other new approaches that have been developed in the fields of human paleontology, physical anthropology, and archaeology. Such techniques were initially based on rather invasive analyses of the specimens, inherited primarily from histology and geochemistry. However, with the rise of non- (or less) destructive methods, this field is rapidly expanding. In the future, study of the actual fossil remains will likely be reserved for the kinds of analyses that cannot be performed on virtual representations. At present, such analyses include, on the one hand, histological approaches mainly addressing bone and tooth microstructures and, on the other hand, chemical analyses addressing either geochronological or paleobiological questions.

Microstructural studies have developed mostly in the field of dental anthropology. The recognition of different types of incremental mineralized structures in the dentine and the enamel since the middle of the twentieth century has led to systematic analyses of their variation in extant and fossil primates (Dean 1987; Stringer et al. 1990; Lieberman 1993; Zhao et al. 2000; Dean et al. 2001; Martin et al. 2003; Schwartz et al. 2003; Smith et al. 2003). This development has been made possible by the improvement of technical equipment such as the scanning electron microscope, the confocal microscope, and computer-assisted microscopy for 3D visualization. The interest in these studies comes from the knowledge that microstructures could be the main, if not the only way, to assess life history in extinct species (Fitz Gerald 1998). This issue has been given increasing attention in an evolutionary perspective since the genetic bases of development have become better understood and their importance for evolutionary changes better appreciated. Future research in this direction will certainly include extensive work on modern variability and more experiments to assess the biological significance of accretional microstructures and their relevance for calibrating the growth patterns of extinct species. Although it is possible to work on externally visible features, such as perikymata (Ramirez Rozzi and Bermudez de Castro 2004), a drawback of these methods is the necessity of slicing precious fossil specimens to analyze fine internal microstructures. However, the technique of thin slicing has greatly improved, and it is possible today to “rebuild” a specimen after analysis following minimal destruction of tissue. In the future, new techniques of imaging may also partly resolve this problem. Although, to date, it remains a very expensive technique, the use of synchrotrons allows access to bone and tooth microstructures without destruction (Tafforeau et al. 2006).

Chemical analyses of fossil specimens have been aimed at reconstructing paleobiological features and are mostly concerned with the extraction of organic molecules. Nonorganic chemical properties of the fossil remains are primarily relevant to the determination of their geological age and are marginally useful in addressing paleobiological issues. To date, DNA and collagen have been the main targets of the research on ancient biomolecules. Techniques based on the use of restriction enzymes have allowed the duplication and subsequent sequencing of tiny and rare fragments of DNA chains. So far, this work has been based primarily on the analysis of mitochondrial DNA, which is smaller and much more abundant than nuclear DNA. The sequencing of a fragment of mitochondrial DNA of the Feldhofer 1 (Neanderthal) specimen in 1997 opened a new era of paleoanthropological studies (Krings et al. 1997). Future development of this research will involve the reconstruction of the entire sequence of the mitochondrial DNA in specimens such as Neanderthals. With the development of new techniques, future work will also address the issue of nuclear DNA in fossil hominids. However, the natural degradation of DNA under given physical conditions imposes a chronological barrier that today seems oddly unsurpassable. Another serious problem in paleogenetic studies comes from the potential for contamination. Paradoxically, the DNA of modern and relatively recent humans remains very difficult to identify as genuine fossil DNA and to distinguish from subsequent contamination (Serre et al. 2004). Studies on the taphonomic processes affecting the deterioration of DNA chains in archaeological or geological deposits may provide an answer to this problem.

Isotopic compositions of the mineral portions of hominid fossils have been used to assess biological issues. These studies face the difficult questions of the taphonomic transformation of the chemical composition of fossils in geological layers (Radosevich 1993; Fabig and Herrmann 2002). Most researchers have thus focused on the more stable component of bone, the protein collagen (Schoeninger 1985; Ambrose 1986; Bocherens et al. 1991, 1997; Richards et al. 2000, 2001). Collagen has been the primary source for the analysis of stable isotopes such as oxygen, nitrogen, and carbon. These isotopes are fixed in the living tissues antemortem, either at an early stage of individual development (e.g., in the teeth) or at some time before death. They are an essential source of information about the environment and the diet of individuals during their lifetimes. One constraint of these studies is that they are limited by the long-term preservation of collagen. For older hominins, carbon fixed in the mineral part of the dental tissues has also been used to investigate what type of plants (C3 or C4) herbivores and their predators extracted their food. One can expect that, as with the study of recent archaeological series, such analyses in the future will bring unexpected knowledge of issues such as migration, seasonality, or even mating strategies among relatively ancient hominids. New research into extracting other longer-surviving proteins, such as osteocalcin, has the potential to provide material for isotopic studies for much older material. An interesting development comes from the combination of microstructural studies and isotopic analyses to assess fine timescale changes in the diet or the environments of fossil individuals (Humphrey et al. 2004). The extension of isotopic analyses to new elements may also lead to interesting developments in this field. For example, sulfur isotopes in collagen, along with strontium and oxygen in minerals, can tell a lot about migration and movement patterns (Nehlich et al. 2010). Isotopic studies (especially of oxygen) will also likely contribute to a much greater knowledge of past environmental conditions and their rapid variation in continental environments, a topic that so far remains much less explored than in oceanic environments and the ice caps.

Understanding Evolutionary Processes

The reconstruction of the evolutionary history of hominoids, and more specifically of fossil humans, has for a long time focused primarily on taxonomic and phylogenetic questions. Important methodological progress has been made in this field during recent decades. In particular, the use of cladistic approaches has provided a better theoretical background. Although these approaches also have their own limitations (Trinkaus 1990), they have become indispensable for assessing the significance and the polarity of features. However, it should be underlined that the development of mathematical techniques to analyze size and shape, including 3D morphometrics, has at times led to the regression of some studies to a precladistic stage. The emphasis placed on the shape distances should not lead researchers to forget that morphological similarity is not a reliable way to analyze phylogenetic relationships when the polarity of the features is not taken into account.

A major problem, discussed extensively in recent years, resides in the features used by paleoanthropologists for cladistic analyses. These discussions have focused on features' significance and relationships either to genetic determinism or to environmental conditions and behavior or to an interaction between the two. Beyond these discussions lie issues such as the independence of such features in their development and their homology when one passes from one species to another (Lieberman 1999; Wood 1999). These are critical questions for the analysis of the fossil evidence and the reconstruction of phylogenetic relationships from a parsimony perspective. However, one may be reasonably optimistic in this matter, as experimental data and a better understanding of the precise genetic and epigenetic mechanisms underlying the development of features will resolve these questions. These may also bring answers to related problems such as the discrepancy sometimes underlined between biomolecular evidence and phylogenetic reconstructions based on the analysis of morphological features of the phenotype (Collard and

Wood 2000; Strait and Grine 2004). They may also bring new light to the debate surrounding modular versus integrative models in the biological development of extinct organisms (Wagner 1996; Wagner and Altenberg 1996; Williams and Nagy 2001; Winther 2001).

As far as the recent stages of human evolution are concerned, it is reasonable to expect that taxonomic and phylogenetic issues will become of minor interest in the future as the main taxa are identified and their phylogenetic relationships understood. However, better understanding of variability, not only in extinct taxa but also in living forms, remains a crucial issue. Although some have predicted the decline of such anatomical studies, it is still striking to contemplate the lack of knowledge of the variability in living humans with respect to many features commonly used in paleoanthropological research. After several centuries of anatomical studies, longitudinal data on the growth and development of many anatomical features is still desperately needed. This lack of data is even more dramatic when one considers the populations of living apes, the closest relatives of humans in the animal world; most of them will likely become extinct in the wild before they have been properly studied.

Research may focus more on paleobiological issues. Changes in growth and development processes during life history, in terms of timing and pattern, are increasingly seen as powerful mechanisms to explain evolutionary changes. Studies of extinct species consider this dimension with increasing frequency, and developmental trajectories will hopefully be identified for different taxa as will the effects of epigenetic phenomena. This is, of course, dependent on an increase in the available paleontological material and also on a greater interaction between paleoanthropology and developmental genetics. 3D morphometrics and other mathematical tools have been identified recently as powerful tools for the reconstruction of those developmental trajectories that can sometimes be modeled (Ponce de León and Zollikofer 2001). Establishing reliable tools to assess the calendar ages of immature individuals in the fossil record is of crucial importance in this matter (Coqueugniot et al. 2004), and developing studies of skeletal microstructure seems an inevitable way to address this problem.

Other aspects of the biology of extinct species might also become accessible through progress in the extraction of biomolecules such as proteins. Osteocalcin has recently been extracted from Neanderthal remains and sequenced (Nielsen-Marsh et al. 2005). In the future, extraction of proteins or lipids from ancient material may even shed new light on the physiology of our ancestors and cousin species. It should also be noted that the extraction of ancient proteins and their sequencing may be extended much further back in time as some of these molecules seem to resist taphonomic degradation much better than DNA.

In recent years, paleodemographic questions have become more and more interesting to paleoanthropologists. Topics such as life history and longevity are critically important to understanding the biological and social adaptations of ancient groups, as well as to addressing questions of learning time during individual life and the transmission of knowledge from one individual to another. Other paleodemographic parameters that appear to be important are the questions of population densities in given areas in a geological time frame and their possible catastrophic variation in relation to environmental changes. Although paleodemographic parameters have long appeared unreachable (Bocquet-Appel and Masset 1982, 1996), different methods of evaluating size fluctuation in ancient populations have emerged from genetic or paleogenetic studies. In addition to providing new understanding of phylogenetic relationships, gene flow between groups, and differences in gene coding for some characters in ancient hominids, paleogenetics has also introduced a new way to assess group size through time in ancient humans (Meyer et al. 2012). Although paleogenetic studies on the Neanderthals did not revolutionize views of their phylogenetic relationships, they did bring a new way to assess genetic variability in ancient populations and, consequently, population size changes (Currat and Excoffier 2004; Serre et al. 2004). The animal models appear to be a tempting alternative for testing demographic fluctuations and their effects on genetic variability during the recent periods of the Pleistocene (Orlando et al. 2002). Such knowledge will allow a better understanding of the possible effects of demographic crashes and genetic bottlenecking on evolutionary processes themselves, as well as the relative roles of genetic drift and natural selection. Combining isotopic analysis and microstructural studies will also allow the garnering of information such as the weaning age of fossil individuals. A fine knowledge of climatic environmental changes, sometimes perceptible on the scale of one human life, also brings new light to the way human populations have adapted biologically and culturally. In this perspective, a better integration of biological and cultural evidence seems necessary for a more thorough understanding of human evolution.

Chronology

The determination of the geological age of fossil hominids is central to paleoanthropological work. Until recently, such determination has centered on the application of radiometric methods to the archaeological context of the discoveries. Although available methods require improvement in their precision and in their calibration, their direct application to hominid specimens also represents major progress, especially for specimens anciently discovered and/or for which the context is unknown or inaccessible. Once more, the development of such approaches has been limited initially by the destructive aspects of these investigations. However, the emergence of new techniques, such as laser ablation, makes the analysis of light or heavy isotopes on precious specimens almost completely nondestructive. In the future, these studies may be applied routinely and become the best way to establish a precise chronology.

As far as the radiometric methods based on C^{14} disintegration are concerned, the development of mass spectrometry has allowed the direct dating of fossil specimens by requiring only small amounts of matter for analysis. Since 2009 the calibration curve for C^{14} dates has been extended back to 50,000 BP, which makes the method more reliable in this time range that is of such crucial importance to the history of modern human dispersal (Reimer et al. 2009). In addition to calibration, contamination remains a major problem and the origin of the sampled carbon must be securely established; methods such as the ultrafiltration of the collagen may allow for the control of this factor. Another future development will be to work with organic carbon from biomolecules such as amino acids that can be identified as genuine fossil molecules belonging to the extinct organisms from which they were extracted. In practice, all this means that many C^{14} dates acquired during the last decades may become meaningless because of the limitations of the techniques used to establish them. Large databases that have been built to process these dates by the thousands and that provide a picture of biological and cultural evolution of humans, especially at the time of the replacement of Neanderthals by modern humans in Europe, can be improved by a critical assessment of the compiled dates. However, the screening process has provided very contrasting pictures and has not satisfactorily solved all questions. This probably results from some bias in the selection process of the data retained, partly depending on the views that different authors have on the evolutionary and peopling processes involved. Eventually, such databases may become obsolete and will need to be rebuilt with more reliable geochronological information.

Picture of an Ancestor

Every human society has built up physicotheological explanations to deal with the question of its origins. In the historical record, such explanations have been furnished by religions and mythologies, but from the middle of the nineteenth century, western societies substituted a scientifically based explicatory model for biblically based explanations. The question of human origins became the concern of scientists rather than priests. However, in 1863, T. H. Huxley, a major supporter of Darwin's views, wrote: "The question of questions for mankind, the problem which underlies all others, and is more deeply interesting than any other, is the ascertainment of the place which man occupies in nature, and of his relationship to the universe of things. Whence our race has come; what are the limits of our power over nature; to what goal are we tending are the problems which present themselves anew, and with undiminished interest, to every man born into the world" (see Huxley 1863, p. 71). Almost 150 years later, this issue is still not free of ideological, if not metaphysical, constraints. This may partly explain why the public has developed such an interest in this field of science. Aside from the inherent attraction of pictures of extinct worlds, any piece of evidence in paleoanthropological studies also becomes a matter of opinion and feeling, even for non-knowledgeable audiences. Prehistory is also consistently the topic of novels, films, and documentaries in which science always has to defend itself against fantasy (Sommer 2006, 2007; Stoczkowski 1994). Museums and educational centers have become incredibly successful with this subject, showing increasing sophistication in their ways of responding to the demands of the public for pictures or 3D reconstructions. Although some of these reconstructions are produced today (Fig. 1) using advanced techniques, they have their own limitations. It is certainly possible to provide reasonable

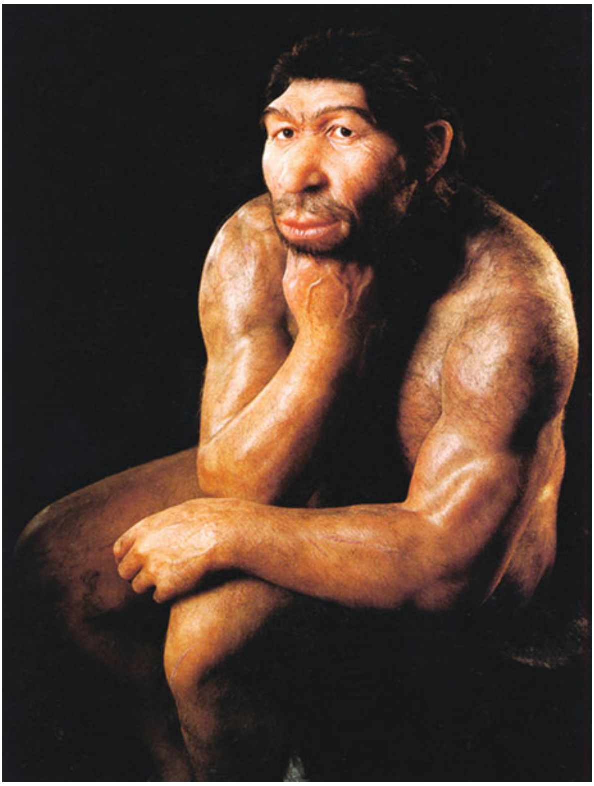

Fig. 1 A reconstruction of a pre-Neanderthal at the Landesmuseum für Vorgeschichte (Halle, Germany). Accurate methods have been developed to reconstruct soft tissues in fossil hominids. However today, like in the past, the picture of ancient humans primarily remains a projection of human fantasies

reconstructions of the general anatomy of well-known fossil species. However, to date, many fine anatomical details, such as skin, hair, and eyes, remain beyond the range of scientific assessment. Unfortunately, they are also of crucial importance to the way other species of humans appear from a modern perspective. The "scientifically based" reconstructions of fossil hominids filling the museums in Europe and America may say much more about the way human diversity is perceived than about the actual aspects of these hominins. In this respect, the progress of the reconstructions since the beginning of the twentieth century may be more limited than is often assumed. Underlying notions of humans as belonging to different species, and possibly contemporaneous in the past, are difficult to integrate, not only for the public but also for scientists from sister disciplines. The humanist framework within which the human and social sciences developed in universities may explain the difficulty that cultural anthropologists and archaeologists, attached to the notion of "uniqueness" of the human being, face in dealing with notions such as ape cultures or the multispecific nature of hominins. More generally, in the post-Second World War era, new conceptions understandably developed around human diversity that provided an ideological framework to which paleoanthropological evolutionary models had to adapt. The questions of Neanderthal nature and abilities and their relationship to extant humans, in other words the last well-documented divergence in the human phylogenetic tree, is one arena in which science and ideological preconceptions have clashed in a complex way.

In this interaction between scientists and the public, the media play an important role. There are many reasons why scientists need to communicate with the public. One is that the interest of the public partly justifies society's investment in this field of pure research. Another may result from more personal reasons. For a department, for a team, for an individual, the visibility of the scientific results obtained becomes increasingly important as it impacts on possible personal promotion and political decisions to support this field of research in general, or a project in particular. Thus, the scientist and the reporter face each other in a dialogue where each needs the other. The reporter needs material for exciting articles; the scientist needs a reporter for publicity (Henke 2010). In the past few decades, this interaction has become increasingly important and has sometimes led to undesirable effects. One obvious pitfall is that the public and reporters are more interested in some issues than in others. Those problems most debated in the media may be of limited interest to the scientific community, and vice versa. Sex between Neanderthals and modern humans is an example of a question universally addressed to paleoanthropologists, and one danger is that, in the need to be well represented in the media, scientists might be led to pander to such questions or even to develop research interests geared to public attention. It is amazing to see how well-developed press services have become, not just in institutions dedicated to public education and communication but also within research structures as well.

Recently these interactions between scientists and the media have entered a new dimension, as personal issues or rivalries between individuals have become of themselves a matter of interest for the press. High-profile international scientific journals have developed "people sections" that deal almost exclusively with these subjects. Reporters have therefore become part of the scientific debate and actors in rivalries, by promoting opinions and sometimes by fueling controversies and conflicts in a way designed to make their articles more exciting.

The Unbalanced Ecology of Paleoanthropology

Paleoanthropology is based on the study of specimens to which access may be difficult. It is also based on sites and fieldwork. The result is that it can be a highly territorial activity, to an extent unequaled in other fields of science. Indeed, aside from scientific problems, the paleoanthropologist must also face a series of political and ethical issues. Although specimens discovered and published a long time ago should be fully accessible to the scientific community, this is not always the case. The situation is even more complex regarding specimens soon after their discovery and/or after a partial description. So far, the scientific community has not established a consensus on resolving such questions. The discoverer of a new specimen has a scientific and moral right to it and is granted priority in providing a scientific analysis of this material, alone or in collaboration with other specialists. However, this well-accepted notion is often blurred by complications. One such complication can result from the multiplicity of the discoverers involved and from lack of agreement at the time of the discovery, or later. And many discoveries occur during the course of archaeological excavations conducted by teams that were not anticipating the possibility of hominin discoveries. Another problem can result from an abusive extension of the time spent between a discovery and the publication of a reasonably comprehensive description of it. The competition that is natural in science is sometimes displayed in a negative form, such as preventing challengers from accessing material, which may be used as a more efficient way to surpass them than producing better scientific results.

Similar situations have developed with respect to site and field access. Most commonly, research teams obtain the monopoly of the study of one site or a geographical area for a certain length of time in order to conduct a defined scientific program. However, apart from this formal arrangement, there are a number of situations where informally and based on political influence, tradition, or nationalistic issues, institutions manage to secure a geographical domain of influence. This is often the case when excavations or field operations are conducted by scientists from western countries in less developed areas. Often, this is facilitated by the fact that the studied areas are located in countries lacking indigenous research in the field of paleoanthropology and/or scientists trained in this discipline. In such cases the work is conducted under the authorization of local administrations that are primarily preoccupied by the conservation of their national patrimony. Here again, different institutions or scientific communities may develop some level of competition in guaranteeing their access to the field. Different countries have developed different regulations restricting the exploitation of archaeological and paleontological material. Situations in which fossil specimens can simply be transferred from the country of their discovery to scientific institutions or museums in Europe or America have almost completely disappeared today.

Many scientists have felt compelled to develop balanced collaborations with the host countries in which they conduct their research, in particular, by helping with the conservation of the material and with the training of local scientists. Furthermore, many countries outside of the western world have managed to develop their own programs and scholars, and the trend is more and more to develop joint projects, although a very unequal equilibrium in terms of financial contribution and/or scientific expertise can lead to bitter conflicts. Although the time of scientific colonialism is over, and in an ideal world, fossils and sites should be accessible to “everyone,” this ideal situation is still far from being reality. Archaeological and paleontological materials are considered as part of the national patrimony in most counties, yet the future of the field lies in fair and fruitful international collaborations.

Conclusion

In summary, although the development of virtual paleoanthropology has opened new venues to access the fossil evidence and to study it, paleoanthropology remains a science primarily centered on objects and sites to which access for researchers is far from being guaranteed. In the last two decades, the field has witnessed spectacular methodological progress providing new insights into the processes of human evolution. However, the question of the origin and nature of humankind remains a sensitive issue. In addressing these questions, science is challenged by many preconceptions.

Cross-References

- ▶ Chronometric Methods in Paleoanthropology
- ▶ Evolutionary Theory in Philosophical Focus
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ Virtual Anthropology and Biomechanics

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Part II

Primate Evolution and Human Origins

Primate Origins and Supraordinal Relationships: Morphological Evidence

Mary T. Silcox, Eric J. Sargis, Jonathan I. Bloch, and Doug M. Boyer

Contents

Abstract

There are five major scenarios that have been advanced to account for the early events in the origination of the order Primates: a transition from terrestriality to arboreality, the adoption of a grasp-leaping mode of locomotion, the evolution of features for visual predation, an adaptation to terminal branch feeding occurring

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M.T. Silcox (✉)
Department of Anthropology, University of Toronto Scarborough, Toronto, ON, Canada
e-mail: msilcox@utsc.utoronto.ca

E.J. Sargis
Department of Anthropology, Yale University, New Haven, CT, USA
e-mail: eric.sargis@yale.edu

J.I. Bloch
Florida Museum of Natural History, University of Florida, Gainesville, FL, USA
e-mail: jbloch@flmnh.ufl.edu

D.M. Boyer
Biological Sciences Building, Duke University, Department of Evolutionary Anthropology, Durham, NC, USA
e-mail: doug.boyer@duke.edu; douglasmb@gmail.com

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during angiosperm diversification, or a combination involving terminal branch feeding followed by visual predation. These hypotheses are assessed using both neontological and fossil data. Of the five scenarios, the angiosperm diversification hypothesis is not contradicted by modern data and is found to be the most consistent with the fossil record. In particular, the evolution of features for manual grasping and dental processing of fruit in the earliest primates (primitive plesiadapiforms), and the subsequent development of features for better grasping and more intense frugivory in the common ancestor of Euprimates and Plesiadapoidea, is consistent with a close relationship between early primate and angiosperm evolution. All the other scenarios are less consistent with the pattern of trait acquisition through time observed in the fossil record. Consideration of non-euprimates (e.g., scandentians and plesiadapiforms) is found to be essential to viewing primate origins as a series of incremental steps rather than as an event.

Introduction: What Is a Primate?

Perhaps the most fundamental issue facing students of primate origins can be summarized by a simple question: what *is* a primate? A clear concept of the diagnosis and taxonomic composition of Primates is essential to providing a coherent understanding of when and why the order separated from the rest of Mammalia. Attempts to define the order Primates have typically started by considering which features of modern primates are present in multiple primate species and are distinctive relative to other mammals. Four major adaptive complexes of traits have been recognized as characteristic of primates of modern aspect (=Euprimates Hoffstetter 1977; see Mivart 1873; Le Gros Clark 1959; Napier and Napier 1967; Martin 1968, 1986, 1990; Szalay 1968; Cartmill 1972, 1992; Szalay et al. 1987):

1. Traits associated with grasping. These include relatively longer hand and foot phalanges, a divergent thumb and big toe, and digits tipped with nails rather than claws.
2. Traits associated with leaping. Although such features have been lost in some extant primates (e.g., *Homo sapiens*), the most primitive euprimates have leaping characteristics that include hind limbs that are long relative to the forelimbs and modified ankle bones.
3. Traits associated with improvements to the visual system. These features include large eyes, convergent orbits, and a postorbital bar or septum. The larger and more complex brain in modern primates compared to other euarchontans may also be associated, in part, with this complex (Barton 1998; Kirk 2006; Silcox et al. 2009b, 2010a). A smaller apparatus for the sense of smell is presumably associated with an increasing reliance on vision as well, leading to a short snout and proportionally reduced related areas of the brain (Silcox et al. 2011).

4. Dental traits associated with herbivory. Relative to specialized insectivores, primates possess teeth that are low crowned, with blunt and bulbous (bunodont) cusps and broad talonid basins, which are features related to eating non-leafy plant materials (e.g., fruit) rather than insects or meat.

Presence of a petrosal bulla has also often been cited as an ordinally diagnostic primate trait (e.g., Cartmill 1972). However, the ubiquity of this feature is questionable since developmental data are required to definitively document it (MacPhee et al. 1983), and its adaptive significance (if any) is unclear.

Defining the order Primates using observations on living taxa as a starting point is problematic because any traits chosen are unlikely to have evolved simultaneously. Instead, a definition that recognizes the process of primate evolution and that encompasses the earliest, possibly stem, members of the order will have greater explanatory power. This problem is discussed further below.

Ecological Scenarios for Primate and Euprimate Origins

Researchers investigating primate origins have typically focused on building an ecological scenario that could explain the evolution of one or more of these adaptive complexes. The earliest such scenario is the arboreal hypothesis of primate origins, which traces its roots back to the work of G. Elliot Smith and F. Wood Jones in the early part of the twentieth century. The arboreal hypothesis was extended and broadly popularized by W.E. Le Gros Clark (1959). In this hypothesis, grasping extremities were seen as having value for more secure climbing, and the distinctive primate orbital features were explained as being useful for judging distances in the trees during leaping.

All the other ecological scenarios that have been developed assume a life in the trees for ancestral primates but seek to go beyond simple arboreality to consider more specific types of behavior. Szalay and colleagues (e.g., Szalay and Delson 1979; Szalay and Dagosto 1980, 1988; Szalay et al. 1987; Dagosto 1988) considered a derived locomotor mode, grasp-leaping, to have driven the evolution of most of the features that characterize euprimates, including those of the visual apparatus. They linked the ability to rapidly jump from branch to branch with the need to be "…subsequently securely anchored" (Szalay and Delson 1979, p. 561) to the landing point. Visual changes were relevant to judging distances in rapid, leaping locomotion (Szalay and Dagosto 1980, 1988: Dagosto 2007). Crompton (Crompton et al. 1993; Crompton 1995; Crompton and Sellars 2007) subsequently argued that acrobatic leaping in euprimates requires visual specializations and that leaping may have evolved as a predator evasion strategy, based on studies of leaping mode and proclivity in modern strepsirhines. In Szalay's hypothesis, anatomical changes for grasp-leaping were preceded by a shift to a more herbivorous diet in primitive primates (i.e., plesiadapiforms) thought to be ancestral to Euprimates (Szalay 1968, 1972; Szalay and Dagosto 1980; Szalay et al. 1987).

Cartmill (1972, 1974, 1992, 2012) focused on visual predation as key to the origin of Euprimates. The visual predation hypothesis as originally conceptualized (see below) linked visual features beneficial to accurately gauging the distance to prey items with grasping hands and feet that could provide both a secure hold on narrow supports and a prehensile apparatus for snatching prey (Cartmill 1974). Because he thought they lacked orbital specializations and grasping features, Cartmill advocated excluding plesiadapiforms from Primates.

Sussman (1991; Sussman and Raven 1978; Sussman et al. 2013) suggested a link between the origin of Primates and the Cenozoic diversification of angiosperms (i.e., trees that produce fruit and flowers). He agreed with Szalay that a key event in early primate evolution was the invasion of the "arboreal mixed feeding adaptive zones" (Sussman and Raven 1978, p. 734) in the Paleocene. This involved increased use of non-leafy plant resources by early primates as angiosperms developed features that made them more tempting to non-insect seed and pollen dispersers, such as specialized flowers and larger fruit. With the appearance of still larger propagative plant organs (e.g., fruit, seeds) near the Paleocene-Eocene boundary, the ancestral euprimates developed features for entering terminal branches to better exploit these resources.

Two major classes of data have been used to assess the relative validity of these various ecological scenarios. The first "tests" various ecological functions assigned to character complexes in the different models using the comparative method (e.g., Kay and Cartmill 1977; but see Bock and von Wahlert 1965; Bock 1977). The second employs the fossil record to document the sequence of anatomical changes that occurred in primate evolution and seeks to tie these changes to adaptive shifts (e.g., Bloch and Boyer 2002; Bloch et al. 2007).

Comparative Method

Cartmill (1970, 1972, 1974) assessed the then prevalent arboreal hypothesis from the point of view of the diversity of modern arboreal animals. He argued that if living in an arboreal habitat could explain the distinctive features of primates, then these traits should also be found in other arboreal forms, and particularly in the arboreal members of groups that also include terrestrial species. Cartmill found that arboreal animals in general do not have features similar to those seen in modern primates. For example, arboreal squirrels are not more primate-like than terrestrial squirrels in certain specialized grasping traits, such as a reduction of the claws, or in vision-related features like the degree of orbital convergence. Nonetheless, arboreal squirrels are successful at many of the same behaviors practiced by primates, including making reasonably long jumps and foraging among slender branches. He argued that forward-facing orbits, while enhancing stereoscopy, decrease parallax and with it the ability to judge distance at longer ranges. For this reason, orbital convergence is not a very useful trait for gauging distances in a jump, but is very effective for visualizing objects close to the face. Based on these comparisons, it seems unlikely that the distinctive adaptive complex of euprimates can be simply linked to a shift to an arboreal mode of life.

Cartmill's hypothesis of primate origins, visual predation, has also been challenged from the standpoint of modern analogy. Sussman (1991; Sussman et al. 2013; see also Crompton 1995) pointed out that most living primates are omnivores, not specialized insectivores. This includes, for example, cheirogaleids (Atsalis 2008), which are often viewed as good living models for the ancestral euprimate (Sussman et al. 2013). What's more, for many primates their methods of prey capture emphasize scent and hearing over vision (Sussman et al. 2013). For example, tarsiers have been observed to capture their prey with their eyes closed (Niemitz 1979), and the most orbitally convergent primates, the lorises, use scent to detect their slow-moving and often smelly prey (Sussman et al. 2013). If living primates are not typically specialized visual predators, it is not clear why one would expect morphologically similar extinct species to be.

Alternatively, some authors (e.g., Sussman and Raven 1978; Sussman 1991; Crompton 1995) have sought analogues for early primates among frugivores, such as Old World fruit bats. The absence of primate-like visual features in some modern visual predators (e.g., mongooses, tupaiid treeshrews, many species of birds; Cartmill 1992; Sussman et al. 2013) and the presence of convergent orbits in some exclusively herbivorous taxa (koalas, sloths, fruit bats, kinkajous; Rasmussen and Sussman 2007; Sussman et al. 2013) suggest that there is no simple relationship between forward-facing orbits and visual predation. A possible "solution" to this criticism that the euprimate-like mechanism of orbital convergence for prey capture is only needed in nocturnal animals (Allman 1977; Cartmill 1992) could be refuted if the earliest euprimates were not nocturnal (see below).

Sussman's (1991; Sussman and Raven 1978; Sussman et al. 2013) angiosperm diversification hypothesis has been criticized based on the lack of an association between the diversification of angiosperms and the evolution of adaptations in arboreal marsupials that converge on those seen in primates (Cartmill 1992). Nonetheless, in a study of the somewhat primate-like South American didelphid marsupial *Caluromys derbianus*, Rasmussen (1990) did find some support for Sussman's model, in that a substantial part of its diet comes from terminal branch fruit feeding in a manner similar to modern primates. Rasmussen and Sussman (2007) found similarly analogous species among the Australian marsupial radiation, including, for example, the pygmy-possum *Cercartetus nanus*. These species do eat insects, which they capture by grasping them with their hands, perhaps providing some support for Cartmill's model; *Cercartetus* in particular has quite convergent orbits (Cartmill 1974). However, *Caluromys* does not have orbits that compare with primates in their degree of convergence (Rasmussen 1990), and a more detailed understanding of the behavior of *C. nanus* has led to its characterization as a flower specialist that only eats insects opportunistically, rather than as a visual predator (Rasmussen and Sussman 2007). These observations substantially weaken the link between convergent orbits and visual predation.

Rasmussen's (1990) study can be seen as providing a fifth, composite scenario for primate origins that has ancestral primates initially venturing out onto terminal branches to find fruit and other plant parts, with the secondary evolution of features for prey capture to capitalize on the insect resources they found in this milieu (Rasmussen 1990; Cartmill 1992).

The grasp-leaping scenario of primate origins (Szalay and Delson 1979; Szalay and Dagosto 1980, 1988; Szalay et al. 1987; Dagosto 1988) is less susceptible to criticisms based on modern analogy than the other ecological scenarios because it does not depend on a general evolutionary relationship for its validity. Rather, it stems from a "fossil-first" approach to considering adaptive change, beginning with the evolutionary transitions documented in the fossil record, and then attempting to determine their adaptive meaning in a form-functional context. This highlights a major contrast in approaches to the question of primate origins among the major participants in the debate. Under Szalay's approach, the unique origins, constraints, and evolutionary histories of different mammalian lineages mean that adaptive explanations applied to one group need not apply to any other. Cartmill, however, argues that "[t]he only evolutionary changes we can hope to explain are. . .*parallelisms*: recurrent modifications that show up over and over again in different lineages for the same structural or adaptive reasons. . ." (Cartmill 1993, p. 226).

One limitation of Cartmill's approach is that it assumes that all adaptive shifts of interest must be parallelisms, because otherwise there would be no possibility of explaining them. This reflects a more general issue with the use of modern analogy to test hypotheses about evolution. Any historical event is by definition a unique occurrence, even if it is more or less similar to other such unique occurrences that have taken place in other lineages. There is no reason to believe that everything that has happened once has happened twice. The evolutionary process that produced primates began at a unique starting point (i.e., the divergence of this clade from the rest of Mammalia), at a particular point in time, with a unique environmental and geographical context, and finished at a unique endpoint (i.e., the diversity of extant species). The starting point was heavily constrained by the evolutionary history of what went before, and the adaptive significance of the features evident at the current endpoint is dependent not only on the current usage of a given trait but also on the biological needs of all the animals that existed along the evolutionary lineage leading to a particular modern species. Modern non-primates that appear similar to primates might have passed through series of adaptive stages quite different from those experienced by primates' distant ancestors and thus may have arrived at their current form by a very different path. For this reason, arguments that ancient marsupials did not acquire their primate-like traits as a result of angiosperm diversification are not directly relevant to the question of whether or not primates did. The study of modern primates, or modern non-primate analogues, in isolation cannot provide a demonstrably accurate picture of the process of primate origins – it can only yield hypotheses that are more or less plausible for subsequent testing by the fossil record.

A somewhat analogous situation occurred in the early history of human paleontology. In the early part of the twentieth century, quite plausible scenarios were proposed that suggested either a large brain or bipedal locomotion as being the first-occurring distinct human trait (Lewin 1987). With the discovery and then acceptance of australopiths (primitive human ancestors with adaptations for bipedal locomotion but relatively small brains; McHenry and Coffing 2000) as hominins any "brains first" scenario was decisively falsified, no matter how plausible it may have seemed on the surface. And so too must any ecological scenario of primate origins be considered falsified, if the predicted pattern of trait acquisition is not matched by the fossil record.

Fossil Record

Primate Supraordinal Relationships

While in a strict sense the origin of Primates was no more dramatic than a single speciation event (Henke and Tattersall 2007; Cartmill 2012), the fossil record suggests that many of the characteristics thought to distinguish Euprimates were acquired incrementally through the first ten million years of primate evolution in the Paleocene (Bloch et al. 2007). It is to this process that the ecological hypotheses for Primate origins apply. Elucidation of this adaptive process relies centrally on knowing the relationships of taxa at the base of the primate tree, to understand the evolutionary steps taken to build the first euprimate.

There is a growing consensus on the broader relationships of Primates within Mammalia. Molecular analyses have fairly consistently recovered a group including Primates, treeshrews (Scandentia), and colugos (Dermoptera; Adkins and Honeycutt 1991; Waddell et al. 1999; Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004). Waddell et al. (1999) suggested the name Euarchonta for this clade. This name makes allusion to an earlier hypothesis of primate supraordinal relationships: the group Archonta, which included bats with these three orders (Gregory 1910; Novacek 1992; McKenna and Bell 1997). Molecular studies have consistently failed to find a close relationship between bats and the other archontans – rather, chiropterans have generally grouped with carnivorans and ungulates (e.g., Pumo et al. 1998; Miyamoto et al. 2000; Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004). As a result, the concept of Archonta sensu lato has fallen out of favor. Rodents and rabbits (Glires) are supported as the closest relatives to Euarchonta (Murphy et al. 2001a, b; Madsen et al. 2001). The resulting clade has come to be known as Euarchontoglires (Murphy et al. 2001b). Euarchontoglires is linked to a clade including ungulates, whales, lipotyphlan "insectivores," carnivorans, and bats (Laurasiatheria) in Boreoeutheria (Springer and de Jong 2001).

Within Euarchonta, there is less of a consensus about the branching pattern among the three ordinal groups. In terms of the sister taxon of Primates, all three possibilities have been recovered in various analyses: Scandentia (e.g., Novacek 1992; Liu et al. 2009), Dermoptera (e.g., Janečka et al. 2007), and Sundatheria (Scandentia + Dermoptera; e.g., Liu et al. 2001; Murphy et al. 2001a, b; Springer et al. 2003, 2004; Bloch et al. 2007; Nie et al. 2008; Ni et al. 2010). In an analysis that combined molecular data with the largest morphological dataset yet compiled for the study of mammalian interrelationships, O'Leary et al. (2013) found strong support for Sundatheria as the sister taxon of Primates. If this hypothesis is correct, it implies that the best model for the ancestor of primates based on extant forms is represented by the reconstructed common ancestor of Euarchonta, not by treeshrews in isolation. In particular tupaiids, the diurnal family of treeshrews often used for comparison to primates (e.g., Beard 1993a), become less relevant as ancestral primate models. The sole living member of the family Ptilocercidae, *Ptilocercus lowii*, is the extant treeshrew closest to the base of Scandentia (Olson et al. 2004, 2005; Roberts et al. 2011) and shares many more features than tupaiids do with dermopterans (Sargis 2001a, 2002a, b, c, d, 2004, 2007). These shared features are present in *Ptilocercus* and dermopterans in spite of some fundamental differences between their locomotor modes (gliding in dermopterans, arboreal quadrupedalism in *Ptilocercus*; Sargis 2001a, 2002a, b, c, d, 2004, 2007), implying that they may be ancestral for the common ancestor of Dermoptera and Scandentia, or even of Euarchonta. As such, *Ptilocercus lowii* might provide the best living model for the common ancestor of Primates (Fig. 1). Even if this hypothesis of relationships is not correct, and either Scandentia or Dermoptera is the true sister taxon to primates, the fact that *Ptilocercus* is consistently recovered as the most basally divergent treeshrew (Olson et al. 2004, 2005; Roberts et al. 2011), coupled with the extremely

Fig. 1 Illustration of *P. lowii*, the pen-tailed treeshrew. This arboreal species may be the best living model for the ancestor of Euarchonta and of Primates (Photo by Annette Zitzmann © 1995)

specialized morphology of all living dermopterans, implies that *Ptilocercus* is probably still the best living model for the common ancestor of Primates.

In terms of extinct taxa, the group most critical to evaluating the supraordinal relationships of primates are the plesiadapiforms. "Plesiadapiformes" is a paraphyletic grouping of extinct fossil mammals known from the Paleocene and Eocene of North America, Europe, and Asia (Russell 1964; Beard and Wang 1995; Fu et al. 2002; Smith et al. 2004; Silcox and Gunnell 2008). Although Tabuce et al. (2004) argued that there was also an African family of plesiadapiforms (Azibiidae), they later revised their interpretation and classified the relevant species into Euprimates as primitive strepsirhines (Tabuce et al. 2009). Represented by over 140 named species classified into 11 families, plesiadapiforms represent a very diverse radiation and form a significant component of the fauna recovered from many Paleocene localities (Rose 1981; Gunnell et al. 1995).

The systematic position of plesiadapiforms has been a matter of long-standing debate. Based largely on dental similarities, most early workers classified plesiadapiforms in Primates, often specifically in Tarsiidae (e.g., Matthew and Granger 1921; Gidley 1923). More recently plesiadapiforms have been thought of as the first radiation of the order Primates, more primitive than any modern group (e.g., Szalay and Delson 1979; MacPhee et al. 1983; Szalay et al. 1987). This idea has been challenged on a variety of fronts. Martin (1968) and Cartmill (1972) advocated removing plesiadapiforms from Primates to allow for a clearer definition of the order. However, in failing to provide a clear alternative classification for plesiadapiforms (beyond dumping them in a wastebasket "Insectivora"), this approach did little to clarify primate supraordinal relationships. Wible and Covert (1987) also suggested removing plesiadapiforms from the order Primates, on the grounds that cranial evidence was more supportive of a scandentian-euprimate tie than a plesiadapiform-euprimate one. They argued that the dental evidence linking plesiadapiforms to euprimates (excluding scandentians) consisted only of ill-defined "trends" (Wible and Covert 1987, p. 9). This conclusion was not based on any *detailed* consideration of teeth, however, which is particularly problematic since the euprimate-plesiadapiform relationship had always been supported largely by dental evidence. And, like earlier objections to classifying plesiadapiforms in Primates, this argument dealt only with the issue of euprimate relationships, without providing any clear resolution to the question of where plesiadapiforms would be classified. Finally, in the early 1990s, an alternative systematic position for plesiadapiforms was suggested by Beard (1989, 1990, 1993a, b) and Kay et al. (1990, 1992), who argued that at least some members of this group (Paromomyidae and Micromomyidae) shared closer ties to Dermoptera than Euprimates. Although these authors agreed on this point, their hypotheses of relationships were in disagreement in virtually every other way, including which taxon was the sister group to Euprimates (Scandentia in the case of Kay et al. 1992; Dermoptera + plesiadapiforms according to Beard 1993a). And, as in Wible and Covert (1987), very little consideration was given to the dentition.

Beard's (1989, 1990, 1993a, b) and Kay and colleagues' (1990, 1992) conclusions have been challenged by numerous studies on both phylogenetic and functional grounds (e.g., Krause 1991; Szalay and Lucas 1993, 1996; Wible 1993; Wible and Martin 1993; Van Valen 1994; Runestad and Ruff 1995; Stafford and Thorington 1998; Hamrick et al. 1999; Bloch and Silcox 2001; Sargis 2002d, 2007; Bloch and Boyer 2002, 2003; Silcox 2001, 2003, 2008; Bloch et al. 2007; Boyer and Bloch 2008). As one example, a key character proffered (Beard 1990, 1993b) in support of a relationship between some plesiadapiforms (paromomyids and micromomyids) and dermopterans to the exclusion of euprimates was unusual hand proportions, with elongate intermediate phalanges (Beard 1990, 1993b). Subsequent discoveries of better-associated plesiadapiform postcranial fossils have demonstrated that this inference was incorrect – the calculated hand proportions were the product of mixing hand and foot bones (Bloch et al. 2007; Boyer and Bloch 2008; see also Krause 1991; Hamrick et al. 1999).

Discovery of numerous new specimens of plesiadapiforms, documenting previously poorly known or totally unknown anatomical regions (Bloch and Boyer 2002, 2003; Bloch and Silcox 2001, 2006; Bloch et al. 2007; Boyer and Bloch 2008; Boyer 2009; Fig. 2), has prompted a reconsideration of plesiadapiform relationships. These data were included in an analysis that sampled the cranium, dentition, and postcranium (Bloch et al. 2007; Fig. 3a) and incorporated observations on *Ptilocercus*. The results of this analysis failed to support the plesiadapiform-dermopteran relationship. Rather, plesiadapiforms formed a paraphyletic stem group at the base of the order Primates. One subset of plesiadapiforms, the plesiadapoids (Plesiadapidae + Carpolestidae + Saxonellidae), was the sister taxon of Euprimates, making them crucial for establishing primitive states for that clade. Results from a subsequent analysis that included a broader sampling of mammals outside Euarchonta and a wider range of cranial and postcranial characters (Silcox et al. 2010b; Fig. 3b) were largely congruent with those of Bloch et al. (2007), apart from some details of the branching order among primitive plesiadapiforms (micromomyids and microsyopids).

One implication of these results is that plesiadapiforms might be best included in the order Primates (Bloch et al. 2007; Silcox 2007), in a return to earlier conceptions of how to define the group (e.g., Szalay 1975; Szalay and Delson 1979; Szalay et al. 1987). This notion has received some support from a previous proponent of the plesiadapiform-dermopteran clade (Kay 2003) and was recently incorporated into papers by workers on opposite sides of the debate over the ecological context of primate origins (Cartmill 2012; Sussman et al. 2013; but see Ni et al. 2010, 2013 for an opposing view).

The ecological scenarios discussed above take as their starting point the common features of modern primates. Plesiadapiforms do not possess all of these traits. If plesiadapiforms constitute the primate stem lineage, discussing “primate origins” then involves dealing with at least two sets of evolutionary transitions – first, the branching off of the primate stem and evolution of the earliest primate (*Purgatorius*; Van Valen and Sloan 1965; Johnston and Fox 1984; Fox and Scott 2011) and, second, the origin of Euprimates. Earlier discussions of “primate origins” that explicitly endeavored to explain only the latter transition (e.g., Cartmill 1972; Rasmussen 1990; Sussman 1991) are inherently flawed in trying to account for the concerted

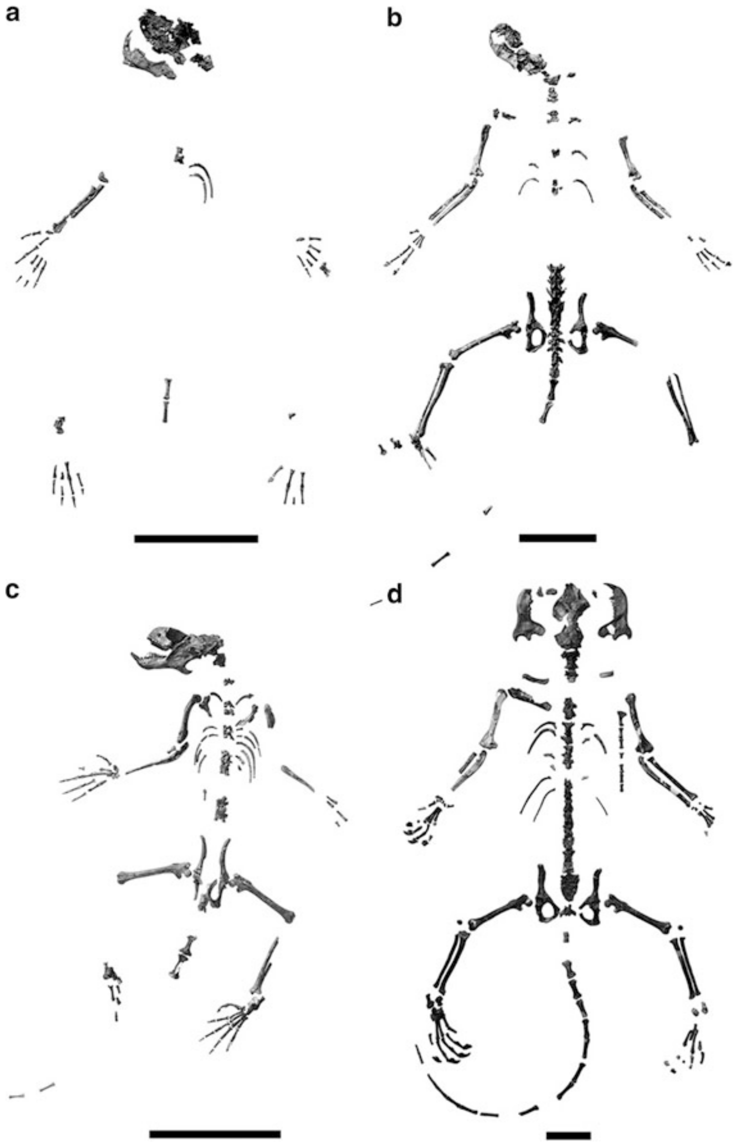

Fig. 2 Skeletons representing three plesiadapiform families were recovered from Late Paleocene limestones (Bloch and Boyer 2007, Fig. 3). Paromomyidae is represented by (**a**) *Acidomomys hebeticus* (UM 108207) and (**b**) *Ignacius* cf. *I. graybullianus* (UM 108210). Carpolestidae is represented by (**c**) *Carpolestes simpsoni* (UM 101963; Bloch and Boyer 2002, Fig. 2a). Plesiadapidae is represented by (**d**) *Plesiadapis cookei* (UM 87990). Scales = 5 cm

evolution of character complexes that did not arise at the same time, mixing the effect of multiple evolutionary transitions. This is true even if one chooses to classify plesiadapiforms as a non-primate sister group to the order.

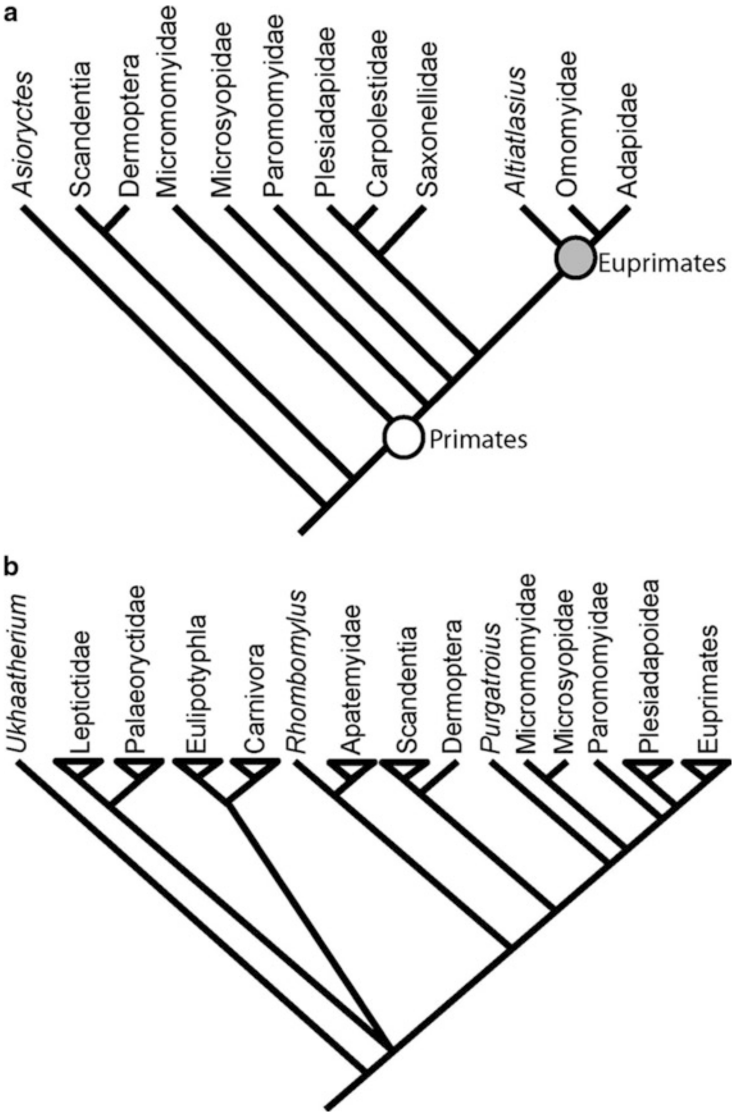

Fig. 3 (**a**) Single most parsimonious tree from a maximum parsimony analysis of 173 dental, cranial, and postcranial characters by Bloch et al. (2007). (**b**) Strict consensus tree of three most parsimonious trees from a maximum parsimony analysis of 240 dental, cranial, and postcranial characters by Silcox et al. (2010b). Note that in both analyses plesiadapiforms form a series of paraphyletic stem taxa at the base of Primates, and Plesiadapoidea is the sister taxon of Euprimates

Using the hypothesis of primate supraordinal relationships given in Fig. 3a, Bloch et al. (2007) tested predictions about the sequence in which anatomical transformations occurred pursuant to the various ecological scenarios (e.g., Cartmill 1992). In the same way that “brains first” scenarios of human origins relied on the evolution of large brains before features for bipedalism, so the ecological scenarios of primate origins require a certain order for the addition of traits through time for them to be considered valid.

Predictions for Ecological Scenarios of Primate and Euprimate Origins

Under the arboreal hypothesis, the prediction is inherent that the evolution of characteristically primate traits coincided with a move into an arboreal habitus. If, on the other hand, the ancestors of primates were already arboreal while lacking such traits, then the arboreal hypothesis would be effectively falsified. It would also be falsified if the evolution of characteristic primate features pre-dated a move to the trees, for example, if forward-facing orbits were found in an animal otherwise adapted for a terrestrial habitus.

The grasp-leaping hypothesis posits a relationship between the evolution of features for grasping and those for leaping. As such, if grasp-leaping is to function as an explanatory hypothesis for euprimate origins, then the evolution of these features should coincide in time. Visual features for improved stereoscopy should also coincide with the adoption of a more rapid, leaping, locomotor mode. Although it may still be true that early euprimates were functionally grasp-leapers, if such a coincident evolution of the relevant traits is not found, then this hypothesis would lose its explanatory power as a central motivating force in euprimate origins.

It is more difficult to generate a set of predictions for the visual predation hypothesis because Cartmill's views appear to have changed through time with respect to how the various distinctive primate traits are supposed to have evolved in the context of this scenario. Cartmill (1974) made an explicit link between the utility of specialized grasping with hindfeet and visual predation: "…these visually guided predators [*Cercartetus* and *Caluromys*] also have grasping hindfeet. The utility of this trait to their way of life is evident" (p. 69). "…it is reasonable to conclude that these novelties ["grasping extremities and large, convergent orbits"] were functionally related…" (p. 70). At the time he apparently did not consider clawlessness per se to be part of this complex: "Reduction of the claws and development of grasping specializations of the hand have occurred independently, in different ways and for different reasons in various primate lineages" (p. 76).

On the other hand, in 1992 Cartmill suggested that grasping extremities and claw loss, he suggested, had also originated as predatory adaptations (Cartmill 1992, p. 107; emphasis ours) based on the habits of small prosimian primates like *Microcebus*, *Loris*, and *Tarsius*, which track insect prey by sight and seize them in their hands. This implies that these features should be tied together temporally, since they were acquired as part of the same adaptive shift to more predatory behaviors.

However, Kirk et al. (2003, p. 741b) claimed that Bloch and Boyer (2002) mis-characterized visual predation suggesting that "[a]s originally formulated (Cartmill 1972), Cartmill's thesis interprets the prehensile, clawless extremities of primates as adaptations for locomotion on slender arboreal supports," and Cartmill (2012, p. 216) stated that "[c]omparative anatomy reveals no necessary connection between grasping hind feet and visual predation." This suggests that

Cartmill now considers visual predation not to be the explanation for the evolution of grasping characteristics in primate evolution in spite of his earlier assertions.

What is impossible to deny, however, is that visual predation is a dietary hypothesis. Since visual predation involves an increasing reliance on insect prey, this should also be reflected in the teeth of the earliest euprimates. This is true even if these forms were grasping prey with their hands rather than with their teeth (contra Cartmill 1972, 1974), because dental features for insectivory reflect not only prey capture but also processing of food items with the unique physical properties of insects. If early primates or euprimates were found to be equally or less insectivorous than their forbears, visual predation would be refuted as a central motivating force in early primate evolution. Since visual predation also relies to some degree on nocturnality (Allman 1977; Cartmill 1992), a finding that the earliest primates or euprimates were diurnal would substantially weaken this hypothesis.

The angiosperm diversification hypothesis predicts two stages in the evolution of primates. First, with the initial exploitation of the arboreal mixed feeding adaptive zone, a dental shift reflecting more use of plant resources should be seen. Second, as the terminal branches were invaded and the use of the food resources from this milieu was intensified, grasping and dental features reflecting these changes should appear. Disassociation between traits for eating fruit or flowers, and those indicating the ability to access terminal branches, would weaken the explanatory power of this hypothesis.

Similarly, the combined hypothesis suggested by Rasmussen (1990), involving first terminal branch feeding on fruit, and then visual predation, requires that “the earliest euprimates had grasping feet and blunt teeth adapted for eating fruit, but retained small, divergent orbits like those of *Plesiadapis*” (Cartmill 1992, p. 111). Subsequent evolution should add features for visual predation, such as forward-facing orbits and teeth with improved capabilities for processing insects, to this basic model. If, however, convergent orbits evolved at the same time as grasping feet or blunt teeth or their appearance was not coincident with the evolution of teeth better designed for eating insects, then this model would be effectively falsified.

Assessment of Ecological Scenarios

With the well-supported pattern of relationships found by the current authors (Bloch et al. 2007; Fig. 3a), it becomes possible to consider the predictions outlined above in light of what is known about the fossil record (Fig. 4). In terms of the arboreal hypothesis, the inferred arboreal habits of all plesiadapiforms known from postcranials (Szalay and Decker 1974; Szalay et al. 1975; Szalay and Drawhorn 1980; Szalay and Dagosto 1980; Szalay 1981; Gingerich and Gunnell 1992; Beard 1989; Bloch and Boyer 2002, 2003, 2007; Bloch et al. 2007; Boyer and Bloch 2008) make it clear that the ancestors of Euprimates were already arboreal. Identification of arboreal features in ankle elements of the most primitive known primate, *Purgatorius*, underlines the antiquity of this feature in the context of the primate radiation (Chester et al. 2012). This is further reinforced by the inclusion of Primates in Euarchonta, because this supraordinal group likely had an arboreal

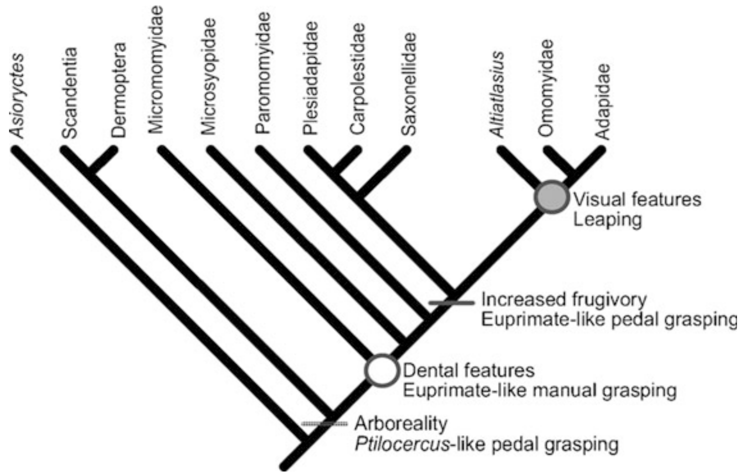

Fig. 4 Results from a maximum parsimony analysis of 173 dental, cranial, and postcranial characters by Bloch et al. (2007), with the most significant evolutionary transitions for primates mapped on. "Dental features" include molars that are low crowned, with bunodont cusps and broad talonid basins (all three of which are related to increased herbivory; Szalay 1968), an enlarged M_3 hypoconulid, and a postprotocingulum (nannopithex or postprotocone fold) on P^4. Evidence for euprimate-like manual grasping includes an increase in the relative length of the digits. Pedal grasping involves the evolution of a divergent big toe with a nail. Visual features include increased orbital convergence and the postorbital bar. Note that these transitions occur in a steplike fashion, with only visual features and leaping being added at the euprimate node

ancestor (Szalay and Drawhorn 1980; Sargis 2001a, 2002e). As such, distinctively euprimate traits cannot be linked to a simple move from a terrestrial to an arboreal habitus. The fact that *Ptilocercus lowii*, an arboreal mammal, may be the best living model for the ancestor of Euarchonta, and thus possibly for Primates (Sargis 2001a, 2002e; Bloch et al. 2003; see above), strongly suggests that arboreality is a feature that evolved prior to the base of the primate radiation (Szalay and Drawhorn 1980). Many of the features that have been cited as possible euarchontan synapomorphies (Szalay and Drawhorn 1980; Szalay and Lucas 1996; Sargis 2002d; Silcox et al. 2005) can also be linked to arboreal locomotion. It is likely that arboreality evolved in the ancestor of Euarchonta (Szalay and Drawhorn 1980; Sargis 2001a, 2002e) and that this trait was retained (but did not originate) in the ancestor of Primates.

The evolution of grasping is central both to the assessment of the grasp-leaping hypothesis and to the visual predation hypothesis as outlined by Cartmill in 1992. With a better fossil record for plesiadapiforms, it is now clear that grasping is not a single character state or set of coordinated transformations. The ancestral euarchontan was likely capable of *Ptilocercus*-like grasping (Szalay and Dagosto 1988; Sargis 2001b, 2002b, e, 2004; Sargis et al. 2007). As Bloch and Boyer (2002, 2003; see also Sargis et al. 2007) demonstrated, the evolution of fully euprimate-like grasping was at least a two-stage process. Features for manual grasping, including relatively long digits of the hand, are present in all plesiadapiforms known from relevant material, with the exception of plesiadapids who are inferred to have secondarily lost this trait (Bloch and Boyer 2002, 2003; Boyer et al. 2004; Kirk et al. 2008; Boyer 2009). Euprimate-like pedal grasping, including an opposable big toe with a nail, is present in *Carpolestes simpsoni* and can be reconstructed as having evolved in the common ancestor of Plesiadapoidea and Euprimates (Bloch and Boyer 2003; Sargis et al. 2007). Although Gebo (2009) took issue with the characterization of the morphology of *Carpolestes simpsoni* as euprimate-like, the shared possession of critical features such as the saddle-shaped distal facet on the entocuneiform for articulation with the first metatarsal, proximal expansion of the medial surface of this facet, and torsion of the first metatarsal (Bloch and Boyer 2002, 2003; Sargis et al. 2007) demonstrates that these groups both possess key elements of the grasping functional complex. As such, Cartmill's (2012, p. 216) assertion that grasping feet "probably evolved independently in *C. simpsoni* and euprimates" is a matter of opinion that has not been demonstrated in a phylogenetic framework.

Plesiadapiforms lack features associated with specialized leaping (Szalay et al. 1975; Szalay and Dagosto 1980; Gingerich and Gunnell 1992; Beard 1989; Bloch and Boyer 2002, 2007; Bloch et al. 2007). *Carpolestes simpsoni*, for example, lacks the relatively long legs typically seen in a leaping mammal, indicating that it was a more generalized arboreal quadruped (Fig. 2c; Bloch and Boyer 2002). The semicircular canal evidence also supports the inference that plesiadapiforms known from cranial material did not use "jerky patterns" of locomotion characteristic of leaping primates (Silcox et al. 2009a). The first primate taxa with some leaping characteristics are early euprimates such as *Cantius*, *Teilhardina*, and *Omomys* (Rose and Walker 1985; Anemone and Covert 2000; Gebo et al. 2012). Although current evidence suggests leaping and visual traits did evolve at the same time, there is a distinct offset between the evolution of features related to grasping and those for leaping. In light of this, although early euprimates were likely grasp-leapers and leaping may have evolved in the ancestral euprimate (Szalay and Dagosto 1980, 1988; Dagosto 1988), the evolution of grasp-leaping was not the event that shaped the origin of Primates or Euprimates.

Similarly, no known plesiadapiforms show any of the specialized features of the orbital system that are associated with euprimate-like vision, including a complete postorbital bar, convergent orbits, reduced snout, or an enlarged and reorganized brain (McKenna 1966; Szalay 1969, 1972; Russell 1964; Kay and Cartmill 1977; Kay et al. 1992; Bloch and Silcox 2006). Therefore, there is an offset between the evolution of grasping and visual features. As such, their coordinated acquisition as part of a shift to a new mode of feeding, visual predation, was not the decisive event in shaping primate or euprimate origins.

It is still possible that adding visual predation to the behavioral repertoire of Euprimates was an important event in the evolution of this group, in which grasping features effectively acted as an exaptation ("preadaptation," Gould and Vrba 1982). There are multiple lines of evidence that lead one to doubt this scenario, however. First, as discussed above, visual predation becomes mechanistically implausible if the earliest euprimates were diurnal (Allman 1977; Cartmill 1992). The primitive activity pattern of Primates is very much in debate. For example, Ni et al. (2004) interpreted a primitive euprimate skull from Asia as having been diurnal. Although there are some problems with this conclusion (Martin 2004; Heesy and Ross 2004; Bloch and Silcox 2006), it draws attention to the fact that the ancestral activity period for euprimates cannot be assumed to have been nocturnal. Indeed, Ankel-Simons and Rasmussen (2008) suggest that early euprimate communities likely included a mix of nocturnal and diurnal species. This would make it difficult to argue that nocturnal visual predation would have been universally important to early euprimates.

Second, if euprimates did undergo a transition to becoming more focused on visual predation, then they should have teeth that are indicative of a more insectivorous diet than their precursors. This is not demonstrably true. The earliest known euprimate, *Altiatlasius koulchii*, has extremely low-crowned teeth with very bunodont cusps (Sigé et al. 1990), which is not consistent with a predominantly insectivorous diet. Of the two best-documented groups of early euprimates, adapoids are usually viewed as being frugivorous and omomyoids as omnivorous (Rose 1995; Bloch and Boyer 2003). The only gut contents known for a primitive fossil primate (the adapoid *Darwinius* from Messel) include fruit remains and no insects. This is likely a real reflection of diet, rather than a taphonomic artifact because in other Messel specimens insect remains preserve well (Franzen and Wilde 2003). Cartmill (2012, p. 216) responded to this objection by suggesting that "[w]e cannot determine which dietary preference is oldest by counting noses." It is certainly true that commonness of a feature does not imply primitiveness (Maddison et al. 1984). However, it is possible to use optimization techniques to infer, from the distribution of traits across a set of relationships, what is most parsimoniously considered to be primitive. Boyer (2007) performed precisely such a test and found no evidence for a shift in dietary behavior toward insectivory at the basal Euprimate node.

What's more, if early euprimates were succeeding and diversifying primarily because they were improving their insect-harvesting abilities, then they should show dental features that indicate that they were at least as well adapted for processing insects as insectivorous mammals living at the same time. This is not the case – most specialized insectivores from the Paleocene and Eocene have much higher crowned teeth and sharper cusps than early primates. It is precisely the absence of such features and the presence of characteristics for processing non-leafy plant material, such as low-crowned molars with broad talonid basins, that makes it possible to separate primitive primate and insectivore teeth in the fossil record. The insectivores most similar to primates in dental form can be reconstructed as having a more omnivorous diet than their specialized insectivorous kin. For example, the erinaceomorph *Macrocranion tupaiodon* from Eocene deposits at Messel, which has superficially primate-like teeth, is known from stomach contents to have eaten not only insects but also plant material and substantial quantities of fish (Storch and Richter 1994).

Cartmill (2012, p. 216) suggested that the fossil record is too incomplete to be used to understand adaptive events around the euprimate node, so that "the main evidence for the ecological correlates of the euprimate peculiarities has to come from functional and comparative anatomy," presumably of extant species. As discussed above, there are numerous incidences of a lack of fit between visual predation and orbital convergence from such studies. Furthermore, there are competing adaptive hypotheses for having convergent orbits. For example, Changizi and Shimojo (2008) argued for a distinct adaptive context for this feature, related to picking out items from a cluttered environment, such as a tree with leaves. These items include any object of greater interest than the clutter, whether it be the location of a branch, a flower, an insect, or a predator. Not only are forward-facing eyes more useful in a cluttered environment, but laterally placed eyes (as in squirrels) are less critical for predator detection since inhabiting a "cluttered" environment also bestows cover from the eyes of hunting predators.

The features suggesting a more herbivorous diet in early primates and euprimates are supportive of the angiosperm diversification hypothesis (Sussman et al. 2013). Within various plesiadapiform lineages and early euprimate groups, improved features for exploiting plant propagative organs continue to appear through the Paleocene and Eocene (Gingerich 1976; Biknevicius 1986; Rose 1995; Bloch and Boyer 2002).

It has been argued (Cartmill 1992) that the angiosperm diversification hypothesis fails to explain the rest of the distinctive traits seen in modern primates (i.e., visual features and leaping). However, Changizi and Shimojo (2008) consider this hypothesis to be consistent with their ideas about the evolution of convergent orbits for differentiating objects in a cluttered environment. Crompton (1995, p. 18) also made this point, suggesting that convergent orbits might have been beneficial in allowing detection of the "small, *and often very inconspicuous"* food items taken by small primates. Cartmill's (2012, p. 217) response to this proposal was to suggest that special visual features are not needed to perceive fruits or flowers because angiosperms advertise their presence with "shiny bright colors and sweet smells." However, it seems important to remember that angiosperms are not advertising their fruit to any possible frugivore. It does an angiosperm no good to have its seeds destroyed or deposited too close to the parent tree, so fruiting trees do not necessarily produce fruit that will be conspicuous to all. Not all fruit in a tropical environment is as easy to see as a domesticated banana.

In terms of leaping, Rasmussen's (1990, p. 273) observations of *Caluromys* also offer a potential explanation for the value of this locomotor mode to a terminal branch feeder: "[t]he grasping and leaping acrobatics exhibited by *C. derbianus* in Costa Rica enabled them to gain access to fruit that was apparently off limits to most of the other nocturnal frugivores of the study area." Perhaps it was refinements to terminal branch feeding technique, offering new access to previously inaccessible food sources and greater abilities for discriminating food choice, that marked the transition to Euprimates.

Rasmussen's combination hypothesis might be seen as offering an alternative to the angiosperm origins scenario that explains, first, the grasping and fruit-eating dental features of basal primates and then the visual characteristics of euprimates. However, this combination hypothesis suffers from the same problems as visual predation in linking the evolution of orbital traits to increased insectivory in the absence of evidence for such a dietary shift. Based on the current evidence, the angiosperm diversification hypothesis applies best to the evolution of early primates. Furthermore, Szalay's (1968) view of the key event in primate origins being a dietary transition to a more plant-dominated repertoire is also supported by the current evidence.

Timing and Place of Origin of Primates and Euprimates

The earliest occurring primate known is *Purgatorius*. Although one possible specimen of this genus is described as coming from the latest Cretaceous (Van Valen and Sloan 1965; Van Valen 1994), it is not a particularly diagnostic tooth (Clemens 2004; Silcox 2008) and comes from a deposit that is time averaged (Lofgren 1995). The earliest, well-dated, diagnostic primate material that has been published in detail pertains to *Purgatorius coracis* from the earliest Paleocene (Pu2) of Saskatchewan (Johnston and Fox 1984; Fox and Scott 2011; see Clemens and Wilson 2012 for a possible even earlier occurrence). Most of the rest of the early primate fossil record is North American, including all definitive micromomyids and palaechthonids, most microsyopids, and all the most primitive paromomyids, carpolestids, plesiadapids, and possibly saxonellid (Fox 1991). Plesiadapiforms have only been known from Asia since 1995 (Beard and Wang 1995), which suggests that this geographic bias may be a sampling phenomenon. The only Asian species that shows relatively primitive plesiadapiform morphology is *Asioplesiadapis youngi* Fu, Wang and Tong 2002 which is similar in some ways to the most primitive families of plesiadapiforms, the Purgatoriidae and "Palaechthonidae," and differs in other ways including having a relatively reduced dental formula (Silcox 2008). As a relatively late-occurring species (early Eocene), *A. youngi* hints at the presence of more primitive lineages of primates in Asia. There remain, however, no Asian taxa as primitive in morphology as North American *Purgatorius*, implying that the fossil record is still most supportive of a North American origin for Primates.

Springer et al. (2012) supported an Asian origin for Euprimates. However, their analysis was based on a molecular phylogeny, without the inclusion of any fossils. Since it is clear that the biogeographic patterns of many mammalian groups have changed over the last 65+ million years, it is critical to consider fossil evidence when assessing the place of origin for any group. Using evidence from the fossil record, Beard (1998) also argued that the origin of Euprimates could be reconstructed as unequivocally Asian. Silcox (2001, 2008) and Bloch et al. (2007) are more conservative in their interpretation of the fossil record, with origins in Asia, Africa, North America, or even Europe being possible in the context of current knowledge. Causes for this equivocation include the African location of the earliest known euprimate, *Altiatlasius koulchii*; the Asian location of the primitive euprimate *Altanius orlovi*; the North American location of much of the primitive plesiadapoid and euprimate record; and the European location of both some early euprimates (e.g., *Donrussellia*) and the poorly sampled plesiadapiform family Toliapinidae, which may be related to early euprimates (Silcox 2001).

The time of origin of Primates and Euprimates can only be minimally constrained using fossil data. As noted above, the earliest known primate, *Purgatorius*, is from the earliest Paleocene (Fox and Scott 2011). In light of the primitive nature of this taxon, the fossil record is not consistent with a date much earlier than this, putting the origin of the group in the earliest Paleocene or latest Cretaceous. The fossil record for mammals more generally suggests a period of very rapid diversification shortly after the Cretaceous-Paleogene boundary (O'Leary et al. 2013).

The earliest occurring euprimate, *Altiatlasius koulchii*, is late Paleocene in age (Sigé et al. 1990; Gheerbrant et al. 1998), implying a divergence for Euprimates before the early Eocene. Furthermore, since the sister group to Euprimates (i.e., Plesiadapoidea) had diverged from their common stem by the latest early Paleocene, Euprimates must be at least that old. Recent molecular dating estimates, which take into account some of the more problematic assumptions inherent in molecular clock models, are starting to approach this timeframe. For example, Springer et al. (2012) estimated that living Primates shared a last common ancestor 71–63 million years ago, which suggests that molecular and fossil datasets are not as divergent as they once seemed (contra Cartmill 2012).

Conclusions: What Is a Primate? (Coda)

When Cartmill developed the visual predation hypothesis, he suggested the removal from Primates of any taxa that lacked modern primate-like orbital and grasping features and thus presumably had not used this mode of feeding (Cartmill 1972, 1974). This was the primary basis for his suggested removal of plesiadapiforms from Primates. Such an approach to defining primates was perhaps an over-optimistic view of the support for visual predation – if, as suggested here, an evolutionary transition to this pattern of behavior is not clearly indicated by the fossil record, then this is surely not an appropriate criterion by which to determine inclusion or exclusion of taxa in the order Primates. This view is underscored by the fact that, of the three "ordinally diagnostic" traits that Cartmill (1972, p. 121) named to diagnose a plesiadapiform-free order Primates – "…the petrosal bulla, complete postorbital bar, and divergent hallux or pollex bearing a flattened nail…" – two are now known in plesiadapoid plesiadapiforms (Bloch and Boyer 2002, 2003; Bloch and Silcox 2006; Boyer 2009). The fossil record demonstrates that the characteristic primate traits listed in the introduction arose in a steplike fashion (Fig. 4). Thus, the criterion that all of these features must be present in a particular taxon for it to be considered a primate is biologically unnatural. Doing so would exclude taxa on the primate stem, which have some, but not all, of these traits, but postdate the divergence of the primate lineage from the rest of Mammalia. As demonstrated above, such stem taxa are critical for understanding the origin and early evolution of Primates, as well as the accumulation and modification of crucial features within this lineage.

As advocates of phylogenetic taxonomy have made clear, there are some distinct advantages to formal taxonomic definitions that are based on specifying a particular ancestor, rather than on a list of mutable characters (Rowe 1987; De Queiroz and Gauthier 1990; Silcox 2007). For this reason, although compiling lists of distinctive primate traits is useful to the process of understanding primate origins, it is inappropriate to consider them formal definitions. Using the precepts of phylogenetic taxonomy, Silcox (2007) suggested the following definition for Primates: “the clade stemming from the most recent common ancestor of *Purgatorius* and Euprimates.”

New discoveries will almost certainly change the prevailing views on the early parts of primate evolution. There is a number of substantial holes in the fossil record for primate origins which, when filled, may fundamentally shift perceptions of primate evolutionary history. First, there is a sizeable spatial discontinuity in the fossils currently available. Plesiadapiforms have only been discovered in Asia in the last 18 years (Beard and Wang 1995). For early euprimates, the few specimens of primitive forms known from Asia and Africa are suggestive of a much larger radiation that is almost completely unknown (Silcox 2001, 2008). Even in North America, the geotemporal patterning of the plesiadapiform and euprimate fossil records means that there are still substantial areas at crucial times that remain unsampled.

Second, some taxonomic groups are also undersampled. Two families of plesiadapiforms, “Palaechthonidae” and Toliapinidae, have the potential to be crucial to an understanding of early primate and euprimate evolution, but both are very poorly known (but see Chester et al. 2011). The best-known plesiadapoids are all relatively derived members of their respective families. In light of the important position of Plesiadapoidea as the sister taxon to Euprimates, finding more, and more complete, primitive plesiadapoid specimens is vital (e.g., Boyer et al. 2004, 2012; Boyer 2009). Perhaps most importantly, a gap still exists between the known plesiadapiforms and the earliest euprimates. No known plesiadapoid has the morphology that would be expected in a euprimate ancestor – they are all too derived in features such as dental reduction, enlargement of the anterior-most incisors, and/or the shape of P_4. Because the earliest plesiadapoids are late early Paleocene in age, Euprimates must have a ghost lineage, stretching through the middle and late Paleocene, which is entirely unsampled. Filling this particular gap will be central to clarifying the evolutionary and adaptive significance of traits for euprimate-like vision and leaping. In light of the complete absence of taxa to fill this gap from the comparatively well-sampled North American record, it seems most plausible that they were living in the Old World.

Finally, since understanding the supraordinal relationships of primates is central to reconstructing events at the base of the order, a better fossil record for other euarchontan groups is also central to the problem of primate origins. As it stands, the Paleogene fossil record for scandentians and dermopterans is virtually nonexistent, with the exception of dentognathic remains that already exhibit peculiarities of extant dermopterans (Ducrocq et al. 1992; Marivaux et al. 2006), fragments of scandentian teeth from the Eocene of China (Tong 1988), and plagiomenids, which may be fossil dermopterans (Bloch et al. 2007; but see Yapuncich et al. 2011). Furthermore, a better understanding of various other fossil groups for whom a tie to Euarchonta, or specifically to Primates, has been suggested (e.g., apatemyids, nyctitheriid insectivores, mixodectids; Szalay and Lucas 1996; Hooker 2001; Silcox 2001; Silcox et al. 2005) has the potential to further clarify the evolutionary events downstream from Primates in the euarchontan evolutionary tree (Silcox et al. 2010b).

Although this discussion of missing data in the fossil record may seem disheartening, the enormous progress that has been made in the last 15 years in understanding primate origins suggests some of these holes may soon be filled. Researchers interested in this topic have moved from a position analogous to that of early anthropologists arguing about whether brains or bipedalism arose first in human evolution, without having any relevant data to choose between the two, to being able to actually test hypotheses about the order of acquisition of traits in early primate evolution. It can only be hoped that continuing diligence on the part of researchers interested in primate origins will serve to fill some of these gaps and allow knowledge of the earliest chapters in human evolution to continue to expand.

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Cross-References

- ▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
- ▶ Fossil Record of the Primates from the Paleocene to the Oligocene
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Molecular Evidence on Primate Origins and Evolution

Ryan L. Raaum

Contents

R.L. Raaum (✉)
Department of Anthropology, Lehman College and The Graduate Center, The City University of New York, Bronx, NY, USA

The New York Consortium in Evolutionary Primatology (NYCEP), New York, NY, USA
e-mail: ryan.raaum@lehman.cuny.edu

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Abstract

Molecular data have become an important source of evidence on primate evolutionary history, particularly when the fossil evidence is limited or lacking. The most recent molecular phylogenetic studies of primate evolutionary relationships and divergence times are reviewed here, primarily at the family level and above. Paleontological data are not entirely omitted, but the focus here is on the molecular results. The current molecular evidence for the branching pattern among the primates, colugos, and treeshrews is presented, and current studies provide weak support for a sister group relationship between primates and colugos. The haplorhine affinities of the tarsier are documented out of a sense of duty; hopefully, it will be possible to stop pretending this is an open question sometime soon. The relationships among the platyrrhine families are quite convincingly resolved in favor of an atelid and cebid clade, but the relationships among *Aotus*, the cebines, and the callitrichines in the Cebidae are poorly resolved. It seems that the molecular evidence will eventually support reciprocal monophyly of the living galagos and lorises, but the molecular data are not presently very helpful. Excluding the early diverging *Daubentonia* lineage, the relationship of the remaining four lemur families almost certainly includes a cheirogaleid-lepilemurid clade but is otherwise poorly resolved by molecular data. Advances in divergence date estimation methodology have begun to rectify some of the absurdly early estimates for the time of origin of the crown primate radiation, but there is still a lot of work to do. Fossil calibration remains problematically applied, and some highly cited studies have poorly justified or unjustifiable calibrations. New methods are being developed for mostly or completely fossil calibration-free divergence date estimation and are very promising.

Introduction

Studies of molecular data have contributed significantly to our understanding of primate origins and evolution, from the seminal immunological studies in the 1960s (Goodman 1961, 1963; Sarich and Wilson 1966, 1967) that contributed to a revision of the hominoid relationships and dramatically shortened the time frame of human evolution to the early years of the DNA era when substantial morphological homoplasy in the Papionini was confirmed from analysis of mitochondrial DNA (mtDNA) sequences (Disotell et al. 1992; Disotell 1994). But what have molecular data done for you lately? In this chapter, the most recent molecular evidence on the higher level relationships of primates is reviewed, from their nearest interordinal relatives to relationships among families and some subfamilies, and presents the most recently published estimates of divergence times.

The ideal molecular phylogenetic study of the primates would include unbiased, genome-wide sequence data from all primate species. These data would be analyzed using the best available phylogenetic reconstruction method; if, as is the case today, there were several well-regarded methods, they would be analyzed using all leading approaches. Any significant discrepancy among the results from the different methods would be investigated and explained. To the extent that primate evolution can be represented by a strictly bifurcating history, a single best estimate of the phylogeny would be presented. Lineage divergence dates (with confidence intervals) would be calculated from evolutionary rate estimates along lineages derived from either well-dated, justifiable calibration points or some other independent rate estimate. No such study has been published. Nothing even comes particularly close. It is an impossible ideal at the moment. Aside from the expense and practical problems associated with collecting sequence data from all primate species, or even all genera, it is not clear that current computational abilities could efficiently analyze the data. Given that current efforts must fall short of the ideal, it is necessary to choose the best estimates among studies with various shortcomings.

For most primate groups, there are now dozens of published phylogenies and divergence date estimates. Given all these choices, it is possible to support quite different evolutionary scenarios by cherry-picking convenient results. One source of this proliferation is that most research groups with a focus on molecular systematics publish series of papers with expanding datasets and new methods. From these series, only the most recently published are presented, unless there are important differences in dataset, question, or analytic method between successive papers from a single author or research group. In addition, no phylogeny or divergence date study published more than a decade ago is given a great deal of weight; these older papers are usually based on very limited datasets and outmoded methods of analysis. The history of the discipline is, of course, important, but the main goal of this review is to update the reader on the most current molecular evidence on primate origins and evolution.

Broader taxon sampling is known to improve phylogenetic reconstruction (Hendy and Penny 1989; Baurain et al. 2007), so the results from studies with broader taxon sampling are prioritized here. However, in the pursuit of the broadest possible taxon sampling, it has become common to create data matrices with large amounts of missing data (e.g., 70 % missing data in Fabre et al. (2009). Whether missing data negatively counteract the benefits of being able to include more taxa is contentious (Misawa and Nei 2003; Lemmon et al. 2009; Simmons 2012; Wiens and Tiu 2012; Roure et al. 2013), and little work has been done on the effect of missing data on divergence date estimation.

Studies that report clearly erroneous topologies are excluded. For instance, not only were Arnason et al. (2008) unable to resolve the phylogenetic position of the tarsier, they placed the colugo (flying lemur) as the sister taxon to the anthropoids within the primates. Of course, some relationships are unknown, and it would be unfair to fault a study that reports a relationship that is now rejected if, at the time the study was published, the relationship in question was truly poorly understood. However, in 2008, even if one only read the molecular systematic literature, it was readily apparent that the tarsier is a haplorhine and colugos are not primates (Goodman et al. 1998; Ziętkiewicz et al. 1999; Murphy et al. 2001b; Schmitz et al. 2001, 2002; Waddell et al. 2001; Janečka et al. 2007).

Admittedly, these criteria are subjective. Therefore, apart from filtering out older studies that have been superseded by more recent publications from the same research groups, studies that are simply outmoded, and publications with dramatically incorrect topologies, data are presented from most broadly sampling primate molecular systematic publications from the last decade. In the figures, those studies that have the best estimates are italicized. In case the reader's preferences differ, information about all of the included divergence date studies (Table 1) and their calibration points (Table 2) are tabulated so that you may make your own informed choices.

Calibration

Most current divergence date estimation methods rely on fossil calibration points, but good calibration is hard to achieve (Raaum et al. 2005; Benton et al. 2009). At the very minimum, a fossil securely within the clade must support any calibrated node. For instance, a fossil used to calibrate the minimum age of the ancestor of the living catarrhines must be attributed by a reasonable consensus of primate paleontologists to the crown catarrhines. This seems obvious, but look through recently used calibrations (Table 2). It should be clear by now that any molecular systematist who attempts to estimate divergence dates using fossil calibration points should be conversant enough with the paleontological literature to be able to cite specific fossil taxa or really must seek out some paleontologist colleagues.

Fossils can only constrain the most recent age of a clade (Hedges and Kumar 2004; Raaum et al. 2005; Benton et al. 2009). If a fossil is properly identified as the earliest member of a clade, then it is not possible for the common ancestor of that clade to have lived more recently. However, there is nothing that can conclusively and usefully constrain the earliest age of a clade. It is possible to absolutely constrain the ancestor of the living catarrhines to sometime after the earliest evidence for land animals, but this is not useful. Despite this, upper bounds on calibration points are common. This ubiquity exists because most divergence dating algorithms require an upper boundary to provide reasonable estimates. For instance, the popular MCMCTree software requires either at least one lower and one upper bound or a calibration distribution that can act as both upper and lower bound (e.g., a normally distributed calibration prior) (Yang and Rannala 2006).

The most commonly used divergence dating algorithms allow the use of probability distributions for calibrations. These probability distributions are an estimate of the likelihood that the true divergence falls within a particular range of dates. For instance, most paleontological data suggests that the most recent common ancestor of humans and chimpanzees lived prior to 5 Ma with no fossils suggestive of common ancestors prior to about 7 Ma. Given these data, it is possible to construct a prior belief (probability distribution) on the likely date of the human-chimpanzee divergence. It is the responsibility of the investigator to ensure that the calibration distribution that is chosen reflects paleontological understanding. For commonly chosen calibration nodes, it might be reasonable to believe that investigators would

Table 1 Summary of divergence dating studies discussed in the text

Study	Focus	Number of primates	mtDNA	nDNA	Dating method	Notes
Bininda-Emonds et al. 2007	Mammals	233	~14,000 bp	~37,000	Local molecular clock (Bailey et al. 1991, Purvis 1995)	Dating method is simplistic and obsolete but given the size of their tree (all mammals) may have been the only practical choice. Only one calibration point within primates
Chatterjee et al. 2009	Primates	219	6,138 bp >40 % missing		Bayesian relaxed clock uncorrelated rates model (BEAST)	
dos Reis et al. 2012	Placentals	32	10,980 bp	20,600,000 bp	Bayesian relaxed clock autocorrelated rates model (MCMCTree)	A tree with divergence dates was estimated from 36 species with nDNA data. The divergence dates estimated on this tree were used as the calibration priors for 274 species with mtDNA data
Fabre et al. 2009	Primates	199–271	8,796 bp 59 % missing	32,493 bp 85 % missing	Bayesian relaxed clock autocorrelated rates model (MULTIDIVTIME)	
Finstermeier et al. 2013	Primates	83	13,281 bp		Bayesian relaxed clock uncorrelated rates model (BEAST)	Used Perelman et al.'s calibrations, many of which are questionable (Table 2)
Hallström and Janke 2010	Placentals	9		2,863,797 bp 21 % missing	Nonparametric relaxed clock autocorrelated rates model (TREEFINDER)	TREEFINDER implements Sanderson's (1997) nonparametric rate smoothing algorithm. The narrow confidence intervals on these estimates reflect only sequence sampling variance and do not include uncertainty in rate estimates. Only two calibration points within primates

(*continued*)

Table 1 (continued)

Study	Focus	Number of primates	mtDNA	nDNA	Dating method	Notes
Hodgson et al. 2009	Platyrrhines	16	10,906 bp		Bayesian relaxed clock autocorrelated rates model (MULTIDIVTIME)	
Horvath et al. 2008	Lemuriforms	32		14,539 bp	Bayesian relaxed clock uncorrelated rates model (BEAST)	Limited calibration (Table 2)
Jameson et al. 2011	Primates	16		505,357 bp <10 % missing	Bayesian relaxed clock autocorrelated rates model (MCMCTree)	
Kitazoe et al. 2007	Placentals	11	3,660 aa		Nonparametric relaxed clock autocorrelated rates model	Branch lengths are estimated by a new method that is designed to correct for convergent evolution. Divergence dates are estimated similarly to Sanderson's (1997) NPRS, but with a cost function that is more tolerant of abrupt rate changes. No calibration points within the primates. Confidence intervals not calculated for most nodes
Masters et al. 2013	Strepsirhines	22	3,529 bp		Bayesian relaxed clock uncorrelated rates model (BEAST)	Calibrated the crown primate node with molecular estimates from Chatterjee et al. (2009) and Perelman et al. (2011), which is not a recommended calibration practice. Dates presented here are from the younger Chatterjee et al. sourced calibration at 77.5 Ma

Matsui et al. 2009	Strepsirhines	26	3,753 aa		Bayesian relaxed clock autocorrelated rates model (MULTIDIVTIME)	Only one calibration point within the primates (Table 2)
Meredith et al. 2011	Placentals	13		35,603 bp 9 % missing 11,010 aa	Bayesian relaxed clock autocorrelated and independent rates models (MCMCTree)	Date estimates are average of estimates from both nucleotide and protein sequence analyses from both autocorrelated and uncorrelated rates models with both hard- and soft-bounded calibrations
Perelman et al. 2011	Primates	186		34,921 bp	Bayesian relaxed clock uncorrelated rates model (BEAST)	Many calibrations are questionable or unjustifiable (Table 2)
Perez et al. 2013	Platyrrhines	28	12,996 bp	34,941 bp	Bayesian relaxed clock uncorrelated rates model (BEAST)	Divergence dates presented here are using the Wildman et al. (2009) topology and the “second hypothesis” calibrations, which does not assume that *Dolichocebus* and *Tremacebus* are crown platyrrhines
Schrago and Voloch 2013	Hominoids	7		560,880 bp	Bayesian relaxed clock uncorrelated rates model (BEAST)	
Schrago et al. 2012	Primates	43	11,672 bp		Bayesian relaxed clock uncorrelated rates model (MCMCTree)	
Schrago et al. 2013	Platyrrhines		~4,200 bp	~156,500 bp 10–15 % missing	Bayesian relaxed clock uncorrelated rates model (MCMCTree)	Dates reported here are from their analysis of molecular data only

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Table 1 (continued)

Study	Focus	Number of primates	mtDNA	nDNA	Dating method	Notes
Springer et al. 2012	Primates	367	9,398 bp >50 % missing	51,801 bp >50 % missing	Bayesian relaxed clock autocorrelated and independent rates models (MCMCTree)	Date estimates are average of estimates from both autocorrelated and uncorrelated rates models with both hard- and soft-bounded calibrations
Steiper and Seiffert 2012	Primates	8		422,687 bp	Bayesian relaxed clock autocorrelated rates model (MCMCTree)	The rate estimates from the Bayesian relaxed clock analysis were regressed against body size and endocranial volume. These regressions were then used to estimate divergence dates from maximum likelihood estimated branch lengths. Dates presented here are the averages from the body size-based estimates.
		61		27,536 bp		
		14		12,478 bp		
		16		5,573,099 bp		
Wilkinson et al. 2010	Primates	15		82,670 bp 13 % missing	Bayesian relaxed clock autocorrelated rates model (MCMCTree)	Calibration prior distributions derive from an explicit model of lineage diversification, fossilization, and fossil recovery

Table 2 Calibration points of primate divergence dating studies

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
Bininda-Emonds et al. 2007	MRCA Haplorhini	>44.5	*Tarsius eocaenus*	Beard et al. 1994	
Chatterjee et al. 2009	MRCA Prosimii	>50.0	*Cantius*	Hartwig 2002	Requires Prosimii to be a valid clade
			Donrussellia		
			Protoadapis		
	MRCA Lemuriformes	>35.6	*Plesiopithecus teras*	Hartwig 2002	Requires Groves' hypothesis of a sister group relationship between *Daubentonia* and *Plesiopithecus* to be correct
	MRCA Lorisiformes	>36.9	*Karanisia clarki*	Hartwig 2002	
	MRCA *Saimiri-Callicebus*	>20.5	*Dolichocebus gaimanensis*	Hartwig 2002	Requires *Dolichocebus* to be a crown cebine
	MRCA Atelidae	>12.6	*Stirtonia* spp.	Hartwig 2002	
	MRCA *Saimiri-Cebus*	>12.1	*Neosaimiri fieldsi*	Hartwig 2002	
	MRCA Anthropoidea	>35.6, offset exponential distribution prior with 95 % of density less than 42.0[a]	*Catopithecus browni*	Hartwig 2002	
	MRCA Cercopithecidae	>10.0	*Microcolobus tugenensis*	Hartwig 2002	
	MRCA *Macaca*	>6.0	*Macaca libyca*	Hartwig 2002	
	MRCA Catarrhini	>20.6, offset exponential distribution prior with 95 % of density less than 30.0[a]	*Morotopithecus bishopi*	Hartwig 2002	
	MRCA Hominoidea	>11.0	*Dryopithecus fontani*	Hartwig 2002	

(*continued*)

Table 2 (continued)

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
	MRCA Homininae	>10.0	*Chororapithecus abyssinicus*	Hartwig 2002	Requires *Chororapithecus* to be a crown hominine
	MRCA *Homo-Pan*	>5.9	*Orrorin tugenensis*	Hartwig 2002	Requires *Orrorin* to be a hominin
dos Reis et al. 2012	MRCA Primates	>55.6, truncated Cauchy distribution with soft lower bounds[b]	*Altiatlasius*	Seiffert et al. 2005	
	MRCA Strepsirhini	33.7–55.6, with soft bounds[c]	*Karanisia*	Seiffert et al. 2009	
	MRCA Anthropoidea	>33.7, truncated Cauchy distribution with soft lower bounds[b]	*Catopithecus*	Seiffert et al. 2005	
	MRCA Catarrhini	23.5–34.0 with soft bounds[c]	*Proconsul*	Tassy and Pickford 1983	
	MRCA Hominidae	11.2–33.7 with soft bounds[c]	*Sivapithecus*	Kappelman et al. 1991	
	MRCA Homininae	>7.25, truncated Cauchy distribution with soft lower bounds[b]	*Chororapithecus*	Suwa et al. 2007	Requires *Chororapithecus* to be a crown hominine
	MRCA *Homo-Pan*	5.7–10.0 with soft bounds[c]	*Orrorin*	Richmond and Jungers 2008	Requires *Orrorin* to be a hominin
Fabre et al. 2009	MRCA Strepsirhini	>38.0		Seiffert et al. 2003, Seiffert 2007	
	MRCA Catarrhini	23.0–33.9		Benton and Donoghue 2007	
	MRCA *Homo-Pan*	>5.7	*Orrorin*	Benton and Donoghue 2007	Requires *Orrorin* to be a hominin

	MRCA Papionini	>6.0		Steiper and Young 2006	Steiper and Young (2006) reference primary paleontology literature by Delson and colleagues to support a papionin divergence by 5–7 Ma
Hallström and Janke 2010	MRCA Catarrhini	23.5–33.7		Benton et al. 2009	
	MRCA *Homo-Pan*	6.5–10.0		Benton et al. 2009	Requires *Orrorin* to be a hominin
Hodgson et al. 2009	MRCA Anthropoidea	>31.5	Fayum catarrhines	Rasmussen 2002; Seiffert 2006	
	MRCA Catarrhini	21.0–30.0	*Morotopithecus* *Victoriapithecus*	Benefit and McCrossin 2002; Young and MacLatchy 2004	
	MRCA Hominidae	12.5–18.0	*Sivapithecus*	Kelley 2002	
	MRCA *Aotus-Saguinus*	>12.5	*Aotus dindensis*	Setoguchi and Rosenberger 1987	
	MRCA *Cebus-Saimiri*	>12.5	*Neosaimiri*	Hartwig and Meldrum 2002	
	MRCA *Homo-Pan*	5.0–8.0	*Ardipithecus* *Orrorin* *Sahelanthropus*	Haile-Selassie 2001; Senut et al. 2001; Brunet et al. 2002; Vignaud et al. 2002	
	MRCA *Theropithecus-Papio*	3.5–6.5	*Theropithecus*	Leakey 1993	

(*continued*)

Table 2 (continued)

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
Horvath et al. 2008	MRCA Lorisiformes	Normal distribution, mean=40.0, sd=1.2[d]		Seiffert et al. 2003	
	MRCA *Homo-Pan*	Normal distribution, mean=6.0, sd=0.5[d]		Kumar et al. 2005	Kumar et al. evaluate variation in the estimate of *Homo-Pan* divergence using other fossil calibrations
Jameson et al. 2011	MRCA Anthropoidea	>34.5, truncated Cauchy distribution[b]	*Catopithecus*	Seiffert 2006	
	MRCA Catarrhini	>20.6, truncated Cauchy distribution[b]	*Morotopithecus*	Gebo et al. 1997	
	MRCA *Homo-Pan*	>7.0, truncated Cauchy distribution[b]	*Sahelanthropus*	Lebatard et al. 2008	Requires *Sahelanthropus* to be a hominin
	MRCA Papionini	>6.0, truncated Cauchy distribution[b]	*Macaca*	Delson, 1992; Delson et al. 2000	
Masters et al. 2013	MRCA Primates	Normal distribution, mean=77.5, sd=8.0[d]		Chatterjee et al. 2009	The time to the MRCA of primates estimated by Chatterjee et al. was used for calibration. There is no fossil evidence directly supporting this calibration. (The Perelmen et al. estimate for this node was also used, but I present estimates only from the Chatterjee et al. calibrated analysis)
Matsui et al. 2009	MRCA Hominidae	13.0–18.0	*Sivapithecus*	Pilbeam et al. 1990; Begun et al. 1997; Ward 1997; Kelley 2002	

Meredith et al. 2011	MRCA Haplorhini	37.1–58.9, implemented as both hard and soft bounds[c]	*Altiatlasius* *Algeripithecus* *Anthrasimias* *Tarsius eocaenus* Eosimiids	Beard et al. 1994; Seiffert et al. 2005; Rossie et al. 2006; Bloch et al. 2007; Bajpai et al. 2008; Prasad 2009; Rose et al. 2009	Although *Altiatlasius*, *Algeripithecus*, *Anthrasimias*, and the eosimiids may not be crown haplorhines (acknowledged by Meredith et al.'s notes on the fossil calibration points), *Tarsius eocaenus* alone can justify this calibration point
	MRCA Lorisiformes	37.1–56.0, implemented as both hard and soft bounds[c]	*Saharagalago* *Karanisia*	Seiffert et al. 2003	
	MRCA Anthropoidea	28.3–56.0, implemented as both hard and soft bounds[c]	*Aegyptopithecus* *Branisella*	Kay et al. 1998, 2008	
	MRCA Catarrhini	20.6–37.3, implemented as both hard and soft bounds[c]	*Afropithecus turkanensis* *Victoriapithecus*	Finarelli and Clyde 2004; Young and MacLatchy 2004; Harrison and Andrews 2009	
	MRCA Hominidae	11.6–28.5, implemented as both hard and soft bounds[c]	*Sivapithecus*	Finarelli and Clyde 2004	
Perelman et al. 2011	MRCA Lorisiformes	Normal distribution, mean=40.0, sd=3.0[d]		Seiffert et al. 2003	
	MRCA Anthropoidea	Normal distribution, mean=43.0, sd=4.5[d]		Poux and Douzery 2004; Franzen et al. 2009	Franzen et al. is the *Darwinius* publication. *Darwinius* (dated to ~47 Ma), whatever it is, is not an anthropoid primate. Poux and Douzery reference Fleagle (1999 [2nd edition of his textbook]) to support an anthropoid calibration at 34 Ma

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Table 2 (continued)

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
	MRCA Catarrhini	Normal distribution, mean=29.0, sd=6.0[d]		Poux and Douzery 2004	Poux and Douzery reference Fleagle (1999 [2nd edition of his textbook]) to support a catarrhine calibration at 20–25 Ma
	MRCA Platyrrhini	Normal distribution, mean=23.5, sd=3.0[d]		Hodgson et al. 2009; Kay et al. 2008	Hodgson et al. does not use a fossil calibration point for the MRCA of platyrrhines (because the whole point of that paper is to estimate that date). Kay et al. is a description of *Dolichocebus* that has "stem platyrrhine" in the title!
	MRCA Papionini	Normal distribution, mean=7.0, sd=1.0[d]		Steiper et al. 2004	Steiper et al. reference primary paleontology literature by Delson and colleagues to support a papionin divergence by 5–7 Ma
	MRCA *Theropithecus-Papio*	Normal distribution, mean=4.0, sd=0.4[d]		Tosi et al. 2005; Ting et al. 2008	Tosi et al. reference primary paleontological literature by Delson and Frost to support a divergence of *Theropithecus* and *Papio* by 4 Ma
	MRCA Hominidae	Normal distribution, mean=15.5, sd=2.5[d]		Matsui et al. 2009	Matsui et al. reference paleontological literature by Kelley, Pilbeam, Begun, Ward, and colleagues to support a split between the orangutan lineage and the African apes between 13 and 18 Ma

	MRCA *Homo-Pan*	Normal distribution, mean=6.5, sd=2.5[d]		Vignaud et al. 2002	Requires *Sahelanthropus* to be a hominin
Perez et al. 2013	MRCA Haplorhini	55.8–65.8, offset lognormal distribution, mean=1.3, sd=0.5 (results in 95 % density in bounds)[e]	*Teilhardina*		
	MRCA Catarrhini	23.5–33.0, offset lognormal distribution, mean=1.5, sd=0.5[e]	*Proconsul*		
	MRCA *Homo-Pan*	5.7–10.0, offset lognormal distribution, mean=0.5, sd=0.5[e]	*Orrorin*		
	MRCA *Saimiri-Cebus*	12.5–26.0, offset lognormal distribution, mean=1.8, sd=0.4[e]	*Neosaimiri*	Stirton 1951; Rosenberger et al. 1991; Takai 1994	This calibration point is from Perez et al.'s "second hypothesis" that does not assume that *Dolichocebus* and *Tremacebus* are crown platyrrhines
	MRCA *Aotus*-Cebinae+Callitrichinae	12.5–26.0, offset lognormal distribution, mean=1.8, sd=0.4[e]	*Aotus dindensis*	Setoguchi and Rosenberger 1987	This calibration point is from Perez et al.'s "second hypothesis" that does not assume that *Dolichocebus* and *Tremacebus* are crown platyrrhines
Schrago and Voloch 2013	MRCA Anthropoidea	Normal distribution, mean=44.0, sd=10.5[d]	*Branisella*	Takai and Anaya 1996	
	MRCA Catarrhini	Normal distribution, mean=28.5, sd=3.4[d]		Benton and Donoghue 2007	
	MRCA Hominidae	9.2–21.9, gamma distribution, shape=15, scale=1	*Lufengpithecus*	Hartwig 2002; Chaimanee et al. 2003, 2004	
			Sivapithecus		
			Khoratpithecus		

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Table 2 (continued)

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
	MRCA *Homo-Pan*	Normal distribution, mean=8.25, sd=0.9^{d}		Benton and Donoghue 2007	
Schrago et al. 2012	MRCA Primates	>55.6	*Altiatlasius*	Tabuce et al. 2004	
	MRCA Strepsirhini	33.7–55.6		Seiffert 2007	
	MRCA Anthropoidea	>33.7	*Catopithecus*	(Simons and Rasmussen 1996)	
	MRCA Catarrhini	23.5–34.0	*Proconsul*	Gebo et al. 1997	
	MRCA Hominidae	11.2–33.7		Chaimanee et al. 2003	
	MRCA Homininae	>7.25			Presumably based on *Chororapithecus*, so requires *Chororapithecus* to be a crown hominine
	MRCA *Homo-Pan*	5.7–10.0		Ruff 2010	
Schrago et al. 2013	MRCA Haplorhini	44.0–60.0	*Tarsius*	Hartwig 2002; Fleagle 2013	
	MRCA Anthropoidea	>26.0	*Branisella*	Takai and Anaya 1996; Takai et al. 2000	
	MRCA Atelidae	>11.0	*Stirtonia*	Hartwig 2002	
	MRCA Cebidae	>10.0		Hartwig 2002	

Springer et al. 2012[f]	MRCA Strepsirhini	37.1–56.0	*Saharagalago* *Karanisia*	Seiffert et al. 2003	
	MRCA Platyrrhini	11.8–37.3	*Neosaimiri* *Laventiana* *Nuciruptor* *Mohanamico* *Aotus dindensis*	Hartwig and Meldrum 2002	
	MRCA Hominoidea	11.6–28.5	*Sivapithecus*	Finarelli and Clyde 2004	
	MRCA Cercopithecoidea	8.5–23.0	*Microcolobus tugenensis*	Benefit and Pickford 1986; Jablonski et al. 2002	
	MRCA *Aotus*-Callitrichinae	11.8–28.5	*Aotus dindensis*	Setoguchi and Rosenberger 1987; Kay 1990; Hartwig and Meldrum 2002; Antoine et al. 2007	
	MRCA *Saimiri*-*Cebus*	11.8–28.5	*Neosaimiri fieldsi*	Hartwig and Meldrum 2002; Antoine et al. 2007	
	MRCA Papionini	5.5–23.0	*Macaca libyca*	Köhler et al. 2000; Jablonski et al. 2002	
	MRCA *Theropithecus*-*Papio*	3.5–16.0	*Theropithecus*	Leakey 1993	
	MRCA *Homo*-*Pan*	5.1–16.0	*Ardipithecus ramidus kadabba*	Renne et al. 1999; Haile-Selassie 2001; Benton et al. 2009	

(*continued*)

Table 2 (continued)

Study	Calibrated node	Constraint	Fossils cited	References cited	Notes
Steiper and Seiffert 2012	MRCA Lorisiformes	>20.0, truncated Cauchy distribution[b]		Seiffert 2007	Used only to generate "weakly calibrated" rate estimates
	MRCA Papionini	6.0–8.0, with hard lower and soft upper bounds[c]	Earliest macaques	Moyà-Solà et al. 2004	Used only to generate "weakly calibrated" rate estimates
	MRCA *Homo-Pan*	6.0–8.0, with hard lower and soft upper bounds[c]	Earliest hominins	Vignaud et al. 2002; Lebatard et al. 2008	Used only to generate "weakly calibrated" rate estimates

[a] See Chatterjee et al. calibration distribution in Fig. 1 as an example

[b] See Jameson et al. calibration distribution in Fig. 1 as an example (Jameson et al. have a hard lower boundary)

[c] In Fig. 1, compare hard bounds of Hallström and Janke calibration distribution to soft bounds of dos Reis et al. distribution

[d] See Perelman et al. calibration distribution in Fig. 1 as an example

[e] See Perez et al. calibration distribution in Fig. 1 as an example

[f] Springer et al. use all of the previously listed calibration points of Meredith et al. (2011) as well

choose similar calibration distributions, but this reasonable expectation is often false. As an example, six different calibration distributions used for the crown catarrhine node within the last 5 years are presented in Fig. 1. This diversity of calibration distributions is not a result of any meaningful disagreement on the paleontological information: most cite fossils dated to about the same time (i.e., *Morotopithecus*, *Proconsul*, *Victoriapithecus*) as the calibration point (Table 2).

In general, somewhat more lenient distributions are preferable, since it seems problematic to exclude a divergence date that would be a good model fit (Yang and Rannala 2006). In the molecular divergence dating literature, this is reflected in the development and preference for "soft"-bounded calibrations (as opposed to "hard"-bounded minimums and maximums that strictly contain calibration dates). The long tails of the Chatterjee et al. (2009), Jameson et al. (2011) and Perez et al. (2013) catarrhine calibrations in Fig. 1 are all examples of soft boundaries where the probability of an older value from the calibration distribution is limited, but nonzero. In addition to these long tails, many divergence dating algorithms allow for some probability density more recent than the calibrating fossil date to accommodate the possibility that the calibration fossil is misdated or mistakenly attributed to the crown group. As an example, in Fig. 1, the Hallström and Janke (2010) catarrhine

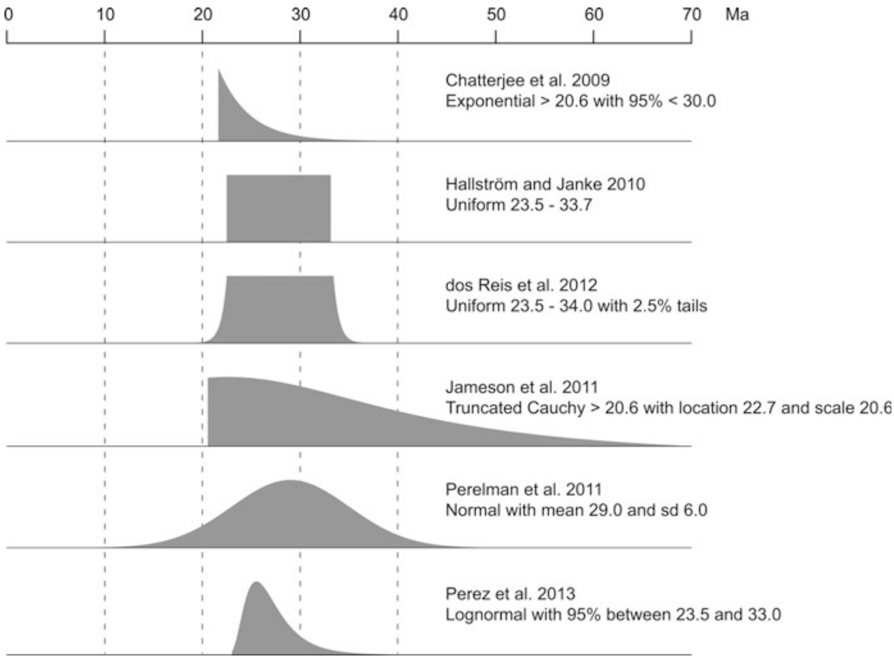

Fig. 1 Examples of various calibration prior distributions. Some examples of calibration density distributions beyond simple minimum or maximum bounds. Distributions may have "hard" boundaries that preclude divergence date estimates at the calibrated node beyond a specified boundary or "soft" boundaries that allow but place low probability on divergence date values outside specified minima or maxima

calibration has hard boundaries, indicating that the model should not be able to choose a divergence date for the calibration node outside the specified minimum and maximum, while the dos Reis et al. (2012) catarrhine calibration extends 2.5 % of the calibration density distribution above and below the specified minimum and maximum.

Given that fossil calibrations are the minimum age of the most recent common ancestor of a clade, a consensus has emerged for the most justifiable calibration distribution shape (Hedges and Kumar 2004; Benton et al. 2009) and the most commonly used software packages for divergence date estimation implement at least one appropriate calibration distribution (Drummond et al. 2006, 2012; Yang and Rannala 2006; Inoue et al. 2010). This preferred calibration density distribution has the most weight nearest the age of the calibrating fossil and a long tail which prioritizes dates nearest the calibration date but accommodates lineages with gaps in the fossil record (i.e., the earliest hominid and hylobatid fossils are found millions of years after most paleontologists believe the hylobatid-hominid divergence occurred). Of the calibration densities shown in Fig. 1 for the crown catarrhine node, those of Chatterjee et al. (2009), Jameson et al. (2011) and Perez et al. (2013) fit this general shape.

Finally, it is important to remember that divergence dates based on fossil calibrations are not estimates of the lineage divergence times but estimates of the minimum age of lineage divergences (Hedges and Kumar 2004; Benton et al. 2009). It is tempting to interpret them as estimates of the time at which the descendant lineages actually diverged, but this would only be true if all of the fossil used for calibrations were among the very first members of the daughter lineages, dated to shortly after the speciation. Because this is almost certainly not true for primate divergence dates, it is important to interpret divergence date estimates as "must have diverged before" rather than "most likely diverged at."

Most of the recently published divergence date estimates are presented, but those studies that best meet good analytic criteria are indicated in the figures. In addition to preferences for recent publications with broad taxon sampling, the following are preferred: studies with dates resulting from clearly justifiable calibration points; studies that use more calibration points within the primates, especially if they are placed at all time depths of the primate radiation (Smith and Peterson 2002; Raaum et al. 2005), and calibration probability density distributions with long tails (see Jameson et al. calibration in Fig. 1); and studies that properly discuss divergence dates as estimates of the minimum age of divergence.

The Place of Primates Within Mammals

Primates' Sister Taxon

Following Gregory (1910), primates were usually classified in the superorder Archonta, along with treeshrews (Scandentia), colugos (Dermoptera), and bats (Chiroptera), and a close relationship of these orders was favored through most of the last century (Simpson 1945; Szalay 1977; Novacek et al. 1988; Novacek 1992; McKenna et al. 1997; Shoshani and McKenna 1998). The demise of Archonta grew out of the proposal that fruit-eating bats (Megachiroptera) might be more closely related to primates than to other bats (Smith and Madkour 1980; Pettigrew et al. 1989). Molecular data collected to test this hypothesis supported bat monophyly but also revealed that bats are not closely related to the other archontans (Bailey et al. 1992; Adkins and Honeycutt 1993; Simmons 1994; Pumo et al. 1998).

The molecular genetic hypothesis of mammalian ordinal relationships was first presented close to its current form in 2001 (Murphy et al. 2001a, b; Waddell et al. 2001). These studies analyzed concatenated data from the mitochondrial genome and 14–19 gene fragments from the nuclear genome to identify four superordinal groups of placental mammals: (1) Euarchontoglires (primates, treeshrews, colugos, rodents, lagomorphs), (2) Afrotheria (aardvarks, elephants, golden moles, hyraxes, sea cows, sengis (elephant shrews), and tenrecs), (3) Xenarthra (anteaters, armadillos, and tree sloths), and (4) Laurasiatheria (artiodactyls, bats, carnivores, cetaceans, gymnures (moonrats), hedgehogs, moles, pangolins, perissodactyls, shrews, and solenodons). All of these groups have received broad support in studies of ever-growing molecular phylogenetic datasets ranging from a handful of short mitochondrial and nuclear sequences to complete mitochondrial sequences to thousands of unlinked nuclear loci (Waddell and Shelley 2003; Nishihara et al. 2006, 2009; Kriegs et al. 2006; Bininda-Emonds et al. 2007; Nikolaev et al. 2007; Waters et al. 2007; Wildman et al. 2007; Hallström et al. 2007; Murphy et al. 2007; Arnason et al. 2008; Prasad et al. 2008; Hallström and Janke 2008, 2010; Meredith et al. 2011; Song et al. 2012b; McCormack et al. 2012; Morgan et al. 2013). Despite large phylogenomic datasets and methodological advances, there is no current molecular genetic consensus on the branching order among Afrotheria, Boreotheria (Euarchontoglires plus Laurasiatheria), and Xenarthra (Nikolaev et al. 2007; Wildman et al. 2007; Churakov et al. 2009; McCormack et al. 2012; Song et al. 2012a; Morgan et al. 2013; Romiguier et al. 2013; Teeling and Hedges 2013).

Within Euarchontoglires, most studies support the clade Euarchonta for primates, treeshrews, and colugos, but the branching order within this clade is not well resolved (Liu et al. 2001; Murphy et al. 2001a, b; Waddell et al. 2001; Janečka et al. 2007; Nie et al. 2008; Perelman et al. 2011). One major impediment to a fully convincing resolution of these relationships is the relative paucity of molecular genetic data for colugos, probably because there are none in captivity. Since it is impossible to meaningfully resolve euarchontan relationships without colugos, only those studies that were able to include colugo data are discussed here. There are two main hypotheses of relationships. In the Primatomorpha hypothesis, primates and colugos are sister taxa (Waddell et al. 2001; Waddell and Shelley 2003; Bininda-Emonds et al. 2007; Janečka et al. 2007; Meredith et al. 2011; Perelman et al. 2011), and in the Sundatheria hypothesis, treeshrews and colugos are sister taxa (Liu et al. 2001; Murphy et al. 2001b, 2007; Nie et al. 2008).

The Primatomorpha hypothesis currently has better support. The strongest evidence comes from Janečka et al. (2007), who find seven amino acid insertion/deletions (indels) that support Primatomorpha and none that support Sundatheria (amino acid indels should be less homoplasious than single nucleotide variants [Simmons et al. 2001]). In addition, in their analysis of ~14 kb of concatenated sequences from 19 nDNA loci, they find consistent support for Primatomorpha when data are included from both families of colugos. That is, broader taxon sampling is required for these groups in order to break up long branches and mitigate the consequences of long branch attraction (Hendy and Penny 1989; Hillis 1996; Pollock et al. 2002).

Long branch attraction can occur in any phylogenetic analysis where two or more of the taxa included are very distant from all other study taxa (i.e., have "long branches") (Felsenstein 1978; Hendy and Penny 1989). In these circumstances, there will usually be relatively few shared, derived characters present in the data matrix to link the long branch taxa to their closest relatives. Even more troublesome, homoplasious resemblances to other taxa may overwhelm homologous ones for these long branch taxa. This misleading homoplasy is more likely in DNA sequence data, because there are only four possible character states for DNA sequence data. Multiple mutations can occur at the same site, resulting in back mutation to the ancestral state or independent mutation to the derived state in another group, and unlike morphological data where convergently acquired characteristics might not be identical on closer inspection, convergently acquired nucleotide characters are identical. Because transposable element insertions and other indels are less likely to converge, these data have been prioritized in resolving the relationships of long branch taxa (Kriegs et al. 2006; Janečka et al. 2007). If there are two or more long branch taxa, they have a good chance of sharing many homoplasious character states and being grouped together. Since outgroup taxa almost invariably have long branches, any ingroup long branch taxa will often be pulled towards the outgroup. Two or more ingroup long branch taxa can also be pulled together. In Euarchontoglires, two of the five orders have long branches in most phylogenetic analyses: the colugos and the treeshrews.

Further support for Primatomorpha is found in Perelman et al.'s (2011) analysis of a mostly independent sequence dataset. Other studies reporting some support of Primatomorpha do not have substantially independent data (Meredith et al. 2011), report varying relationships across different methods of phylogenetic reconstruction (Waddell et al. 2001), or are based on very limited colugo or treeshrew data (Waddell et al. 2001; Bininda-Emonds et al. 2007). While Murphy et al. (2001b, 2007) did initially report support for Sundatheria, these results are superseded by later publications from this research group supporting Primatomorpha (Janečka et al. 2007; Meredith et al. 2011). The sole non-contraindicated molecular support for Sundatheria is found in a chromosome rearrangement reported to be shared by treeshrews and colugos (Nie et al. 2008), but the limited chromosome map generated in this report is more intriguing than convincing.

Dating Primate Origins

Paleontological data suggest that both inter- and intraordinal diversification of placental mammals occurred after the Cretaceous-Paleogene (K-Pg) event (Archibald and Deutschman 2001; O'Leary et al. 2013). In contrast, most molecular studies have reported dates before the K-Pg event for both interordinal splits and at least some intraordinal diversification (Janke et al. 1994; Hedges et al. 1996; Easteal and Herbert 1997; Kumar and Hedges 1998; Arnason et al. 2000, 2001; Springer et al. 2003).

Estimates of the minimum time of the strepsirhine-haplorhine split fall into two groups (Fig. 2). The majority present minimum divergence dates falling between 58 and 72 Ma (Kitazoe et al. 2007; Chatterjee et al. 2009; Hallström and Janke 2010; Jameson et al. 2011; Meredith et al. 2011; dos Reis et al. 2012; Springer

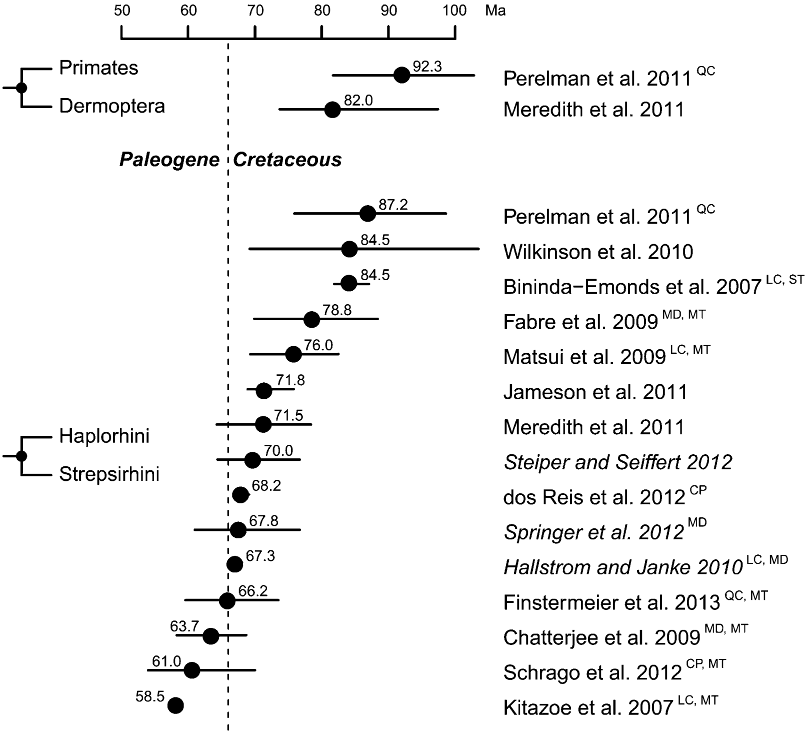

Fig. 2 Divergence date estimates at the base of the Primatomorpha and the Primates. Point divergence date estimates and 95 % confidence/credibility intervals from recent studies. Article citations in italics best meet the quality criteria discussed in the Introduction. Abbreviations following citations are as follows: *CP* calibration point, *LC* limited calibration within primates (see Table 2); *MD* >20 % missing data, *MT* based largely or solely on mtDNA sequences, *ST* supertree-based analysis, *QC* questionable calibration (see Table 2)

et al. 2012; Steiper and Seiffert 2012; Finstermeier et al. 2013), most of which have confidence intervals wide enough that they cannot definitively be said to pre- or postdate the K-Pg event. The second set of divergence dates fall well into the Upper Cretaceous between 78 and 92 Ma and definitively predate the K-Pg event (Bininda-Emonds et al. 2007; Arnason et al. 2008; Fabre et al. 2009; Wilkinson et al. 2010; Perelman et al. 2011).

One of the most innovative studies among those cited above is Steiper and Seiffert (2012). Recognizing the problems with fossil-calibrated divergence date estimation, particularly for earlier divergences where the fossil record can be sparse, Steiper and Seiffert sought to estimate divergence dates with minimal dependence on fossil dates for calibration. Their method takes advantage of the observation that the neutral rate of molecular evolution is correlated with generation time (Wu and Li 1985; Li et al. 1996; Yi et al. 2002; Tsantes and Steiper 2009). And because generation time is correlated with brain and body size (Calder 1984; Harvey and Clutton-Brock 1985; Deaner et al. 2002), the fossil record can be used to inform a model of molecular evolutionary rate change over time.

Steiper and Seiffert first modeled the evolutionary history of body and brain size in primates using data from extant and extinct primates. Second, they verified that brain and body size can explain a substantial proportion of the variance in evolutionary rate across the living primates. Finally, they combined their evolutionary models of brain and body size evolution with their models predicting the rate of molecular evolution from brain and body size to predict evolutionary rates through primate evolutionary history, which provides estimates of divergence dates. While they do use some fossil calibrations (Tables 1 and 2) to generate their initial estimates of molecular evolutionary rates in primate evolution, they deliberately use very few calibration points in order that rate variation across lineages is minimally accounted for by the usual fossil-calibrated divergence dating methods. To the extent that Steiper and Seiffert (2012) accurately model evolutionary rate variation through primate evolutionary history, the divergence date estimates from their method are estimates of the actual date of genetic divergence, rather than estimates of the minimum date of genetic divergence. As such, they can be more directly and correctly interpreted.

Because the identification of the closest living relative of primates has been contentious and colugo data is so limited, there are only two estimates for the primate-colugo divergence that are the most recent estimates from independent molecular systematic research groups and derive from analyses that include data from all euarchontans (Fig. 2). Both of these estimates are well before the K-Pg event, but there is reason to believe that they are overestimates. Meredith et al. (2011) present an estimate of 82.0 Ma (95 % CI: 73.7–97.4), and Perelman et al. (2011) place the primate-colugo divergence at 92.3 Ma (95 % CI: 81.7–102.8). However, both Meredith et al. and Perelman et al. estimate strepsirhine-haplorhine divergence dates that are considerably earlier than almost all other estimates for this node as well (Fig. 2). Nonetheless, the primate-colugo divergence must predate the haplorhine-strepsirhine divergence, and since all estimates of the minimum age of strepsirhine-haplorhine divergence lie near the K-Pg event, it seems most likely that the primate-colugo divergence predates the Paleogene.

Future Directions

The limited evidence for colugos is the major impediment to resolving euarchontan relationships and refining the timing of primate origins. Since there are no captive colugos, it is certainly more difficult to collect DNA from this order. However, while they are geographically restricted to Southeast Asia, they are neither endangered nor particularly rare (there is a free-ranging population of Sunda colugos on the grounds of the Singapore Zoo). Acquiring data from both genera of colugo, the Sunda colugo (*Galeopterus*) and the Philippine colugo (*Cynocephalus*) should be prioritized in order to break up the long colugo branch (these species are estimated to have diverged about 20 Ma [Janečka et al. 2008]). More data are available for treeshrews, including draft genomes for two northern treeshrews (Fan et al. 2013). However, most of the available genetic data available for treeshrews is from *Tupaia* (Tupaiidae), and it should be a priority to obtain more data from smooth-tailed treeshrews (*Dendrogale*, Tupaiidae) and pen-tailed treeshrews (*Ptilocercus*, Ptilocercidae). These genera diverged from *Tupaia* approximately 30–50 and 50–70 Ma, respectively (Roberts et al. 2011). Collecting more sequence data from *Dendrogale* and *Ptilocercus* species will help to break up the long treeshrew branch. Of course, new fossils of early crown primates, especially from the Paleocene, would be very desirable and useful as well.

Haplorhine Relationships and Diversification

Tarsiers Are Haplorhine Primates

The molecular data clearly show that anthropoids are the sister group to tarsiers (Goodman et al. 1998; Ziętkiewicz et al. 1999; Schmitz et al. 2001, 2002; Matsui et al. 2009; Jameson et al. 2011; Lindblad-Toh et al. 2011; Hartig et al. 2013). Much of the early molecular phylogenetic research in primates was based on the analysis of mitochondrial DNA sequences and often showed tarsiers as the sister taxon to the strepsirhines. However, tarsiers have retained some ancestral features in their mitochondrial DNA. In both DNA nucleotide composition and amino acid usage, the tarsier shows a pattern that is more like that seen in non-primate placental mammals and strepsirhines (Waddell et al. 2001; Schmitz et al. 2002; Matsui et al. 2009). In addition, tarsiers have a long independent evolutionary history, which leads to long branch attraction problems in phylogenetic reconstruction. The haplorhine affinity of tarsiers has been recently reaffirmed by analyses of a 1.25 Mb nDNA sequence alignment (Jameson et al. 2011), a genome-wide study of transposable elements (Hartig et al. 2013), and whole genome sequences (Lindblad-Toh et al. 2011).

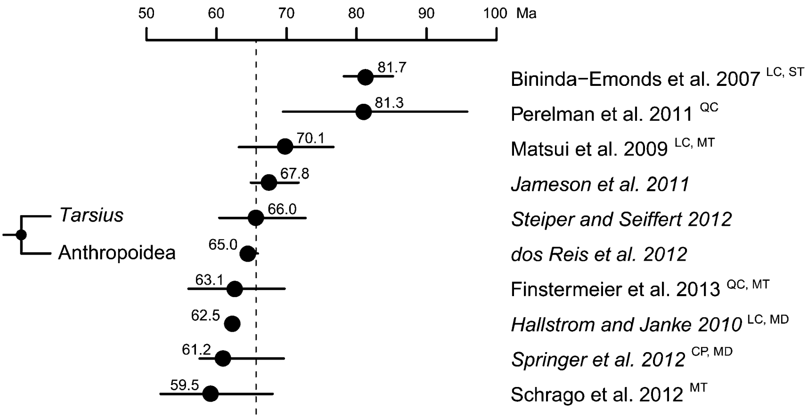

Fig. 3 Crown haplorhine divergence date estimates. Abbreviations and italics as described in the caption to Fig. 2

Dating the Tarsier-Anthropoid Divergence

There are two clear clusters of tarsier-anthropoid divergence times (Fig. 3). A majority of recent studies report that the most recent date of the tarsier-anthropoid divergence lies between 61 and 70 Ma (Matsui et al. 2009; Hallström and Janke 2010; Jameson et al. 2011; Meredith et al. 2011; dos Reis et al. 2012; Springer et al. 2012; Steiper and Seiffert 2012; Finstermeier et al. 2013). Most of these estimates have 95 % confidence intervals compatible with a post-K-Pg diversification of the primates. There are two clear outlier estimates for this divergence date at 82 Ma: one from the placental evolution-oriented supertree study of Bininda-Emonds et al. (2007) and the other from the questionably calibrated study of Perelmen et al. (2011).

Anthropoid Diversification

There are two major branches of the anthropoids, the Catarrhini (Old World monkeys and apes) and the Platyrrhini (New World monkeys or neotropical primates). It is universally agreed across recent molecular dating studies that the catarrhine and platyrrhine lineages must have diverged before the end of the Eocene (Fig. 4). Of course, since the Eocene is the longest epoch of the Cenozoic, this is not altogether satisfying. The best estimates indicate that anthropoid diversification began before 35–45 Ma (Kitazoe et al. 2007; Jameson et al. 2011; dos Reis et al. 2012; Springer et al. 2012; Steiper and Seiffert 2012; Perez et al. 2013; Schrago et al. 2013). The major molecular phylogenetic questions within the anthropoids are the relationships among the platyrrhine families and the time of their diversification and the timing of catarrhine diversification.

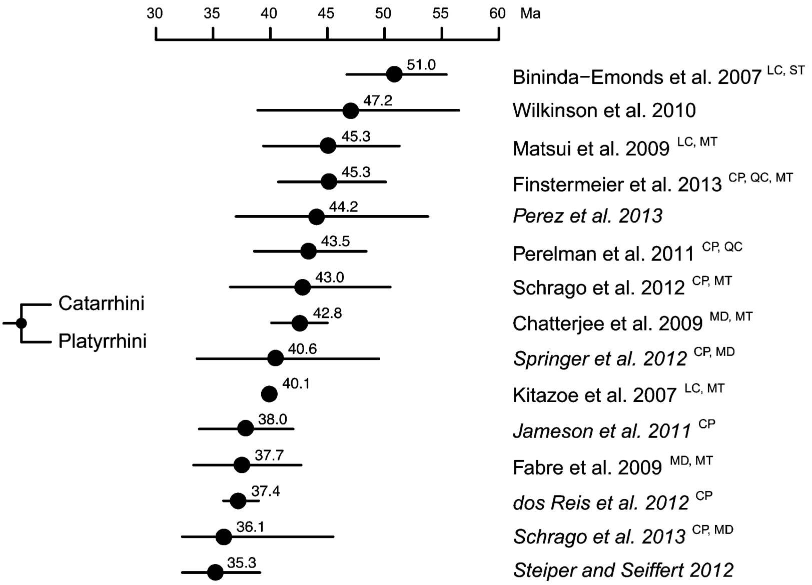

Fig. 4 Crown anthropoid divergence date estimates. Abbreviations and italics as described in the caption to Fig. 2

Relationships of the Major Platyrrhine Lineages

There is broad agreement that there are three major clades of platyrrhines: the Atelidae (spider monkeys, howler monkeys, woolly monkeys, and muriquis), the Cebidae (capuchins, squirrel monkeys, owl monkeys, marmosets, and tamarins), and the Pitheciidae (titi monkeys, sakis, and uakaris) (Goodman et al. 1998; Opazo et al. 2006; Wildman et al. 2009; Perez et al. 2012; Schrago et al. 2012). Early molecular studies reported conflicting relationships among these three families, with some support for all three options: a close relationship of the Atelidae and Pitheciidae (Schneider et al. 1993, 1996, 2001; Harada et al. 1995; Porter et al. 1997, 1999; Goodman et al. 1998; Horovitz et al. 1998; Canavez et al. 1999; Opazo et al. 2006), a close relationship of the Cebidae and Pitheciidae (Schneider et al. 1996; Barroso et al. 1997), and a close relationship of the Atelidae and Cebidae (Chaves et al. 1999; von Dornum and Ruvolo 1999; Steiper and Ruvolo 2003; Ray et al. 2005; Opazo et al. 2006).

There is now a clear consensus that Atelidae and Cebidae are sister taxa (Fabre et al. 2009; Hodgson et al. 2009; Osterholz et al. 2009; Perelman et al. 2011; Perez et al. 2012; Schrago et al. 2012, 2013; Springer et al. 2012; Finstermeier et al. 2013). This conflicts with the earlier molecular publications, the majority of which supported Atelidae and Pitheciidae as sister taxa. The reason for this conflict is that much of the early platyrrhine molecular phylogenetics was based on a handful of nDNA sequences (IRBP, vWF, G6PD, B2M, HBE1), analyzed individually in the earlier papers, then in combination in the later papers. Unfortunately, three of those loci (IRBP, B2M, HBE1) have gene trees that conflict with parts of the platyrrhine species tree. Analyzing any of these three separately or in combination leads to misleading topologies. Even worse, combinations of sequences from other loci with these three often resulted in mistaken phylogenetic inference (e.g., Schneider et al. 2001). Only with the collection of complete mtDNA sequences (Hodgson et al. 2009; Schrago et al. 2012; Finstermeier et al. 2013), rare insertion events (e.g., SINEs) (Ray et al. 2005; Osterholz et al. 2009), and data from dozens of additional nDNA loci (Wildman et al. 2009; Perelman et al. 2011; Springer et al. 2012; Schrago et al. 2013) were the misleading gene trees of these early sequencing targets revealed.

Relationships Within the Cebidae

The owl monkeys, *Aotus*, are difficult to place. All recent molecular phylogenetic studies have found them to be related to the other members of the Cebidae but have reported *Aotus* variably as the sister taxon to the cebines (capuchins and squirrel monkeys) (Wildman et al. 2009; Finstermeier et al. 2013; Schrago et al. 2013), as the sister taxon to the callitrichines (marmosets and tamarins) (Chatterjee et al. 2009; Fabre et al. 2009; Hodgson et al. 2009; Perelman et al. 2011; Schrago et al. 2012; Springer et al. 2012; Finstermeier et al. 2013), or as the sister taxon to a clade containing both the cebines and the callitrichines (Wildman et al. 2009; Perez et al. 2012).

By citation count alone, it would seem that recent molecular work comes down in support of a sister taxon relationship between *Aotus* and the callitrichines. However, many of these studies are based entirely or largely on mtDNA sequences. Wildman et al. (2009) have the best data of all of the cited studies; they collected 11 new independently evolving, putatively neutral, single copy nDNA sequences. (Most of the nDNA loci analyzed in other studies are sequences of functional, adaptive, or biomedical interest.) In their analysis of the newly collected data alone, they recovered *Aotus* as the sister taxon to a cebine-callitrichine clade, but when they combined these new data with previously published genic nDNA sequences, they recovered *Aotus* as the sister taxon to the cebines. Both groupings had low support.

Wildman et al. analyzed concatenated data, which has been the usual approach to multi-locus data (de Queiroz and Gatesy 2007). With concatenated data, different data partitions (sets of sites, codons, loci, etc.) are modeled with different evolutionary parameters (substitution rates, base composition, etc.), but all are evaluated on the same tree topology. This is not ideal. As noted above in the discussion of the relationships among the platyrrhine families, individual loci have histories that can and do differ from each other and the species tree (Pamilo and Nei 1988; Maddison 1997). Until recently, inference of the species tree from a combined analysis of multiple, independent gene trees has been impractical, but computational advances and new methodological developments have now made this approach feasible in what is called the "multispecies coalescent" (Degnan and Rosenberg 2009; Edwards 2009; Ting and Sterner 2013). Perez et al. (2012) reanalyzed the

Wildman et al. data in the multispecies coalescent framework (as implemented in *BEAST [Heled and Drummond 2010]) and recovered the same result as Wildman et al. (*Aotus* as the sister taxon to a clade containing the cebines and callitrichines). Of course, in and of itself, this is not particularly interesting. But Perez et al. also reanalyzed a subset of the Perelman et al. (2011) data matrix (trimmed to minimize missing data while retaining at least one member of each platyrrhine genus) and recovered the same topology as Wildman et al. (which is not what Perelman et al. found in their original *concatenated* analysis). The sole remaining non-mtDNA-based support for grouping *Aotus* and the callitrichines comes from Springer et al. (2012), but this paper is not substantially independent from Perelman et al. (Springer et al. collected sequences from an additional 15 loci and concatenated them with the 54 loci in the Perelman et al. dataset). It seems likely that if Perez et al. repeated their multispecies coalescent analysis with data from the Springer et al. collection, they might still recover *Aotus* as sister to a cebine-callitrichid clade.

Divergence Dates Within the Platyrrhines

The most heated question in the timing of the platyrrhine radiation is the antiquity of the crown lineages (Delson and Rosenberger 1984; Rosenberger 2002, 2010; Kay et al. 2008; Hodgson et al. 2009; Rosenberger et al. 2009; Kay and Fleagle 2010; Perez et al. 2013). The earliest platyrrhine fossils (i.e., *Branisella*) are found in late Oligocene deposits dated to around 26 Ma, but the available material is relatively limited and cannot be convincingly linked to any specific living platyrrhine (Takai et al. 2000). The next earliest fossils are dated at 20 Ma and lie at the heart of the debate about the age of the crown lineages. *Dolichocebus gaimanensis*, from the early Miocene of Argentina (Kay et al. 2008), has been linked to the living cebines (*Saimiri* and *Cebus*) (Rosenberger 1979; Tejedor 2008), perhaps specifically to *Saimiri* (Rosenberger 1979). *Tremacebus harringtoni*, also from the early Miocene of Argentina (Hershkovitz 1974; Kay et al. 2004), has been linked specifically to *Aotus* (Rosenberger 2002; Tejedor 2008). The attribution of these early fossil platyrrhines to crown groups has been termed the “Long Lineages Hypothesis.” My colleagues and I dubbed the alternative – that these early platyrrhines are not closely related to any specific living platyrrhine – the “Successive Radiations Hypothesis” (Hodgson et al. 2009).

For any variant of the Long Lineages Hypothesis to be possible, the specifically linked living lineage must have diverged from its nearest relative by at least 20 Ma. In the most specific linkage, if *Dolichocebus* is most closely related to *Saimiri* among the living forms (Rosenberger 2002), then the *Saimiri* lineage must have split from the *Cebus* lineage by 20 Ma. If *Dolichocebus* is not linked specifically to *Saimiri* but to the larger cebine clade, then the cebines must have diverged from their nearest relative by 20 Ma. Finally, if the hypothesis is simply that *Dolichocebus* could fall *somewhere* within the crown platyrrhines, then the deepest diversification of the living lineages must have occurred by 20 Ma. The same line of reasoning follows for *Tremacebus* with appropriate substitutions for the putative relatives.

It seems reasonable to believe that molecular divergence date estimates could provide some insight into the question of whether or not these early platyrrhines might belong to the crown radiation, and several studies have commented on that hypothesis (Hodgson et al. 2009; Schrago et al. 2012, 2013; Perez et al. 2013). Unfortunately, as discussed towards the beginning of this review, divergence date estimates should usually be read as "are estimated to have diverged before" and cannot provide very strong evidence to exclude an earlier fossil taxon from a crown group, except when there is a large discrepancy (i.e., if the crown group is estimated to have diverged prior to 5 Ma and the questionable fossil is dated at 25 Ma, it seems very likely that it is not part of the crown group). What are required are divergence dates that estimate the actual date of lineage bifurcation rather than minimum dates of bifurcation. Of all the divergence date estimates presented here, those of Steiper and Seiffert (2012) come closest to estimating actual divergence dates (as discussed earlier in the "Dating Primate Origins" section). While their method of date estimation does start with a time-calibrated tree, they did not use any fossil calibrations within the platyrrhines. A second calibration-free set of divergence dates are provided by Perez et al. (2013), who apply a variation of the Steiper and Seiffert method to platyrrhine divergence date estimation.

Focusing on the calibration-free and nearly calibration-free methods, there is an immediate discrepancy. Steiper and Seiffert (2012) estimate that the crown platyrrhines diverged between 17.9 and 20.2 Ma, and Perez et al. (2013) report 20.3–28.5 Ma (Fig. 5). There are too many differences in the details of the procedures that these two studies followed to be able to pinpoint the source of their differences and select a preferred estimate. The Perez et al. estimate of the time to the most recent common ancestor of the living platyrrhines would not directly

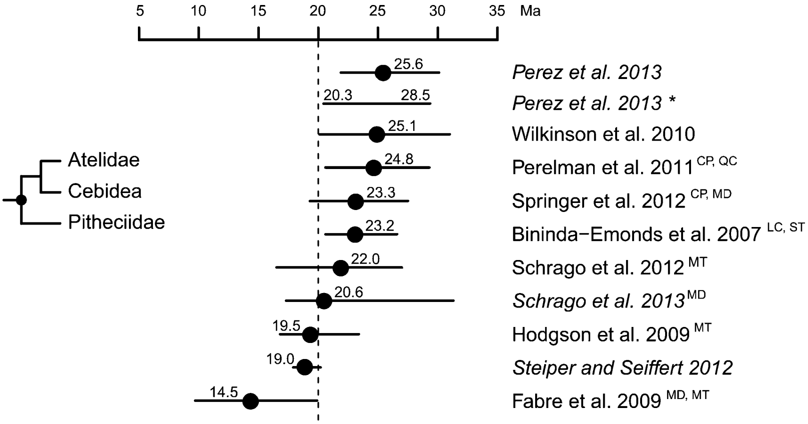

Fig. 5 Crown platyrrhine divergence date estimates. The *dashed line* at 20 Ma indicates the age of the disputed fossil platyrrhine taxa *Dolichocebus* and *Tremacebus*. *Asterisk* indicates the fossil calibration-free divergence date estimates of Perez et al. (2013) as discussed in the text. Abbreviations and italics otherwise as described in the caption to Fig. 2

exclude any of the fossil forms from the crown radiation, while the Steiper and Seiffert estimates would clearly exclude *Branisella* from the crown group but could include *Dolichocebus* and *Tremacebus*.

For the crown Cebidae, Steiper and Seiffert (2012) estimate a divergence between 15.9 and 17.8 Ma, and Perez et al. (2013) estimate 15.6–21.8 Ma (Fig. 6). Again, there is a discrepancy in these date estimates that has consequences

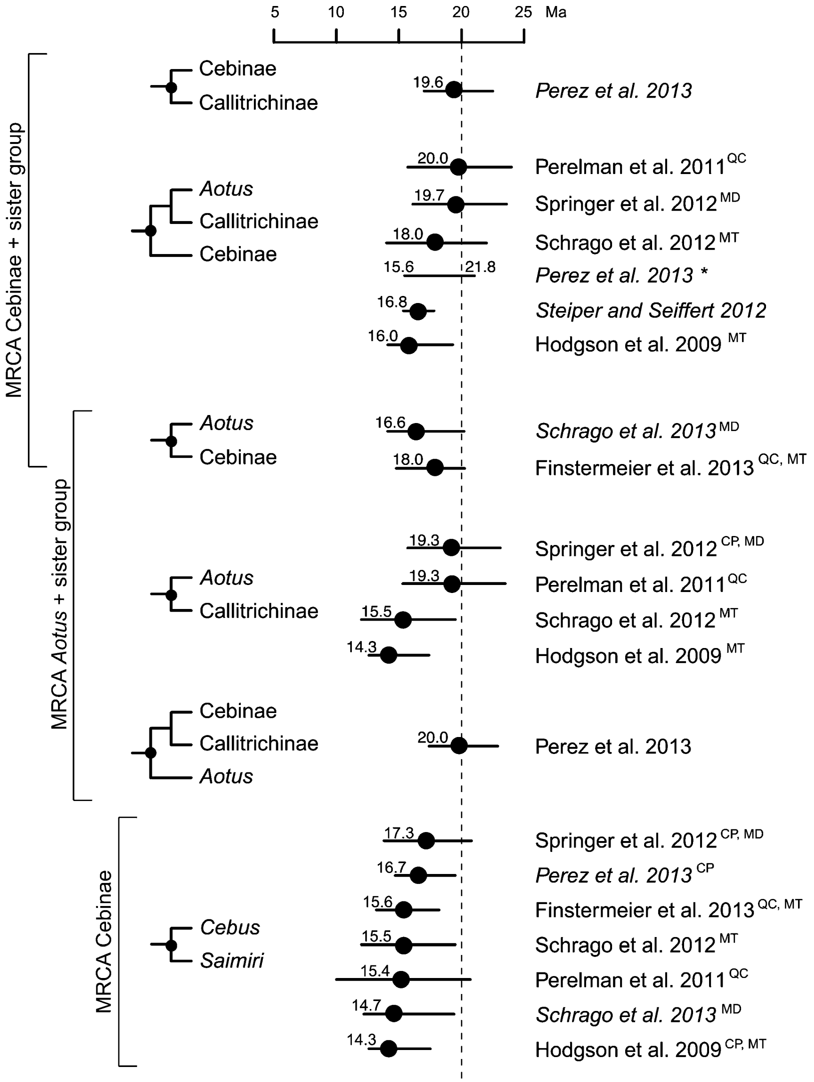

Fig. 6 Divergence date estimates of and within the crown Cebidae. The *dashed line* at 20 Ma indicates the age of the disputed fossil platyrrhine taxa *Dolichocebus* and *Tremacebus*. *Asterisk* indicates the fossil calibration-free divergence date estimates of Perez et al. (2013) as discussed in the text. Abbreviations and italics otherwise as described in the caption to Fig. 2

for our possible interpretation of the early Miocene fossils. Steiper and Seiffert's date clearly excludes *Dolichocebus* and *Tremacebus* from the crown cebids, while Perez et al.'s date range could include them. However, the Perez et al. range only *just* extends deep enough in time to potentially include *Dolichocebus* and *Tremacebus*. If any earlier fossils of these forms were to be found, they would become excluded. Furthermore, while Perez et al. did not present divergence dates within Cebidae (i.e., the *Cebus*-*Saimiri* and the *Aotus*-sister taxon divergences), it seems possible that those date estimates could exclude *Dolichocebus* from the *Saimiri* lineage and *Tremacebus* from the *Aotus* lineage.

Divergence Dates Within the Catarrhines

There is no disagreement on higher level relationships within the catarrhines. There are two superfamilies, the Cercopithecoidea (Old World monkeys) and the Hominoidea (apes and humans), each of which has two subdivisions. The Old World monkeys are split between two subfamilies, the Colobinae (colobines and langurs) and the Cercopithecinae (baboons, guenons, and macaques), while the hominoids are split between the Hylobatidae (small apes: gibbons and siamang) and the Hominidae (great apes: orangutans, gorillas, chimpanzee, bonobo, and human).

The best estimates of the divergence of the cercopithecoids and hominoids range from 23 to 28 Ma (Fig. 7) (Hallström and Janke 2010; Jameson et al. 2011; dos Reis et al. 2012; Springer et al. 2012; Steiper and Seiffert 2012; Schrago and Voloch 2013), consistent with the hypothesis that catarrhine diversification began during the late Oligocene. *Kamoyapithecus*, from deposits dated at 24–28 Ma, is often mentioned as a possible early hominoid (Boschetto et al. 1992; Leakey et al. 1995) and, if so, could be one of the earliest members of the group. However, *Kamoyapithecus* is very fragmentary and may well be a stem catarrhine (Harrison 2002). More recently, both an early stem ape, *Nsungwepithecus gunnelli*, and an early stem Old World monkey, *Rukwapithecus fleaglei*, have been reported from deposits dated at just before 25 Ma (Stevens et al. 2013). While the fossil material from both is very limited, their date is consistent with the 23–28 Ma range from the best recent molecular estimates and could represent some of the very earliest members of each superfamily. Within the hominoids, the best estimates place the split between the smaller and larger apes at 17–21 Ma (Fig. 8) (Springer et al. 2012; Schrago and Voloch 2013). The earliest possible hylobatids are not found until the late Miocene (Jablonski and Chaplin 2009) and the earliest putative stem hominids only begin to appear after 13 Ma (Moyà-Solà et al. 2009; Casanovas-Vilar et al. 2011). Thus, molecular divergence estimates suggest at least 4 Ma of currently undocumented hominid evolution.

There is a broad range in the estimated dates for the divergence between the colobines and cercopithecines from 11 to 24 Ma (Fig. 8). All of the estimates greater than 20 Ma are based on the analysis of mtDNA data alone, so it seems that there is a problem estimating the date of this node from mtDNA, possibly related to the changing substitution rate within the sister hominoid clade (Goodman 1961, 1963, 1996;

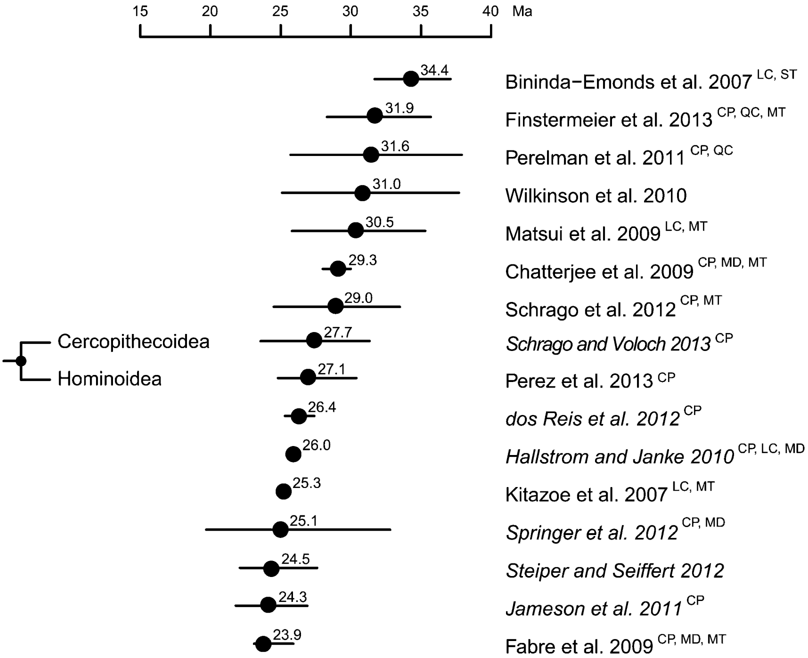

Fig. 7 Crown catarrhine divergence date estimates. Abbreviations and italics as described in the caption to Fig. 2

Steiper et al. 2004). All estimates based on datasets including or entirely comprised of nDNA sequences are less than 18 Ma, and the best of those are between 11 and 14 Ma (Jameson et al. 2011; Springer et al. 2012; Steiper and Seiffert 2012). Recently, Rossie et al. (2013) reported on two isolated cercopithecoid molars from Kenya dated at 12.5 Ma and tentatively assigned them to an unknown colobine genus. These teeth are contemporaneous with the best current molecular divergence date estimates and could either represent some of the earliest colobines or indicate that the molecular estimates should be recalibrated for a slightly older cercopithecine-colobine divergence.

Future Directions

Of the platyrrhine phylogenetic questions presented here, the one least resolved is the branching order among *Aotus*, the cebines, and the callitrichines. While the topology with *Aotus* as the sister taxon to a cebine plus callitrichine clade has been presented as best supported by molecular data, this topology does not have particularly strong support. Since there are fairly substantial mtDNA and nDNA data available for these taxa, there may have been a rapid diversification at the origins of the Cebidae or reticulation and hybridization following the initial diversification. The second least resolved platyrrhine systematic question is whether or not the late

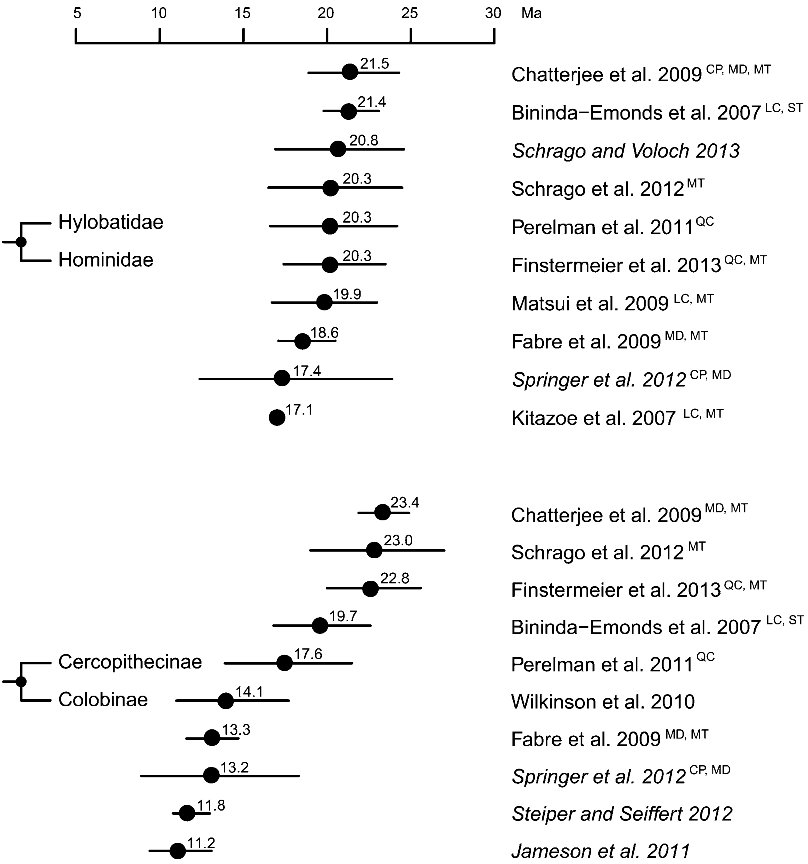

Fig. 8 Crown cercopithecoid and hominoid divergence date estimates. Abbreviations and italics as described in the caption to Fig. 2

Oligocene and early Miocene fossil platyrrhines belong to the crown radiation, they cannot easily be resolved with molecular data, primarily because most current divergence date estimates require fossil calibrations and as a result are minimum divergence dates only. Divergence dates that are mostly or entirely independent of fossil calibration data suggest that the early Miocene forms could be crown platyrrhines, but are less supportive of relating these forms to specific extant genera. Ultimately, this is a problem that will primarily be resolved in the paleontological literature (Kay et al. 2008; Kay and Fleagle 2010; Rosenberger 2010).

Within the catarrhines, there are no higher level phylogenetic questions that are unresolved, and divergence date estimates are beginning to converge on similar values. The major unresolved questions for catarrhine primates lie in the relationships among genera within (sub)families and the relationships of species within genera. Is the kipunji (*Rungwecebus*) more closely related to *Lophocebus* mangabeys or baboons (Burrell et al. 2009; Zinner et al. 2009; Roberts et al. 2010)? What are the relationships among the hylobatid genera (Chan et al. 2010, 2012, 2013; Israfil et al. 2011; Meyer et al. 2012; Wall et al. 2013)? What are the relationships among the colobine genera and are the African colobines paraphyletic (Sterner et al. 2006; Karanth et al. 2008; Osterholz et al. 2008; Roos et al. 2011; Liedigk et al. 2012; Wang et al. 2012)?

Strepsirhine Relationships and Diversification

Divergence of the Lemuriform and Lorisiform Strepsirhines

Estimates for the divergence of the lemuriform and lorisiform lineages range from 49 to 73 Ma (Fig. 9). Four estimates from studies with questionable calibration, based mostly or solely on mtDNA sequence data, or with limited calibration within the primates can probably be dismissed out of hand (Bininda-Emonds et al. 2007; Fabre et al. 2009; Matsui et al. 2009; Perelman et al. 2011). The remaining studies provide estimates between 49 and 57 Ma, with the best ranging from 51 to 56 Ma (Hallström and Janke 2010; Jameson et al. 2011; dos Reis et al. 2012; Springer et al. 2012; Steiper and Seiffert 2012). These early Eocene dates for the lemuriform-lorisiform divergence seem to be generally compatible with current paleontological interpretations of strepsirhine origins (Switek 2010; Maiolino et al. 2012; Seiffert 2012).

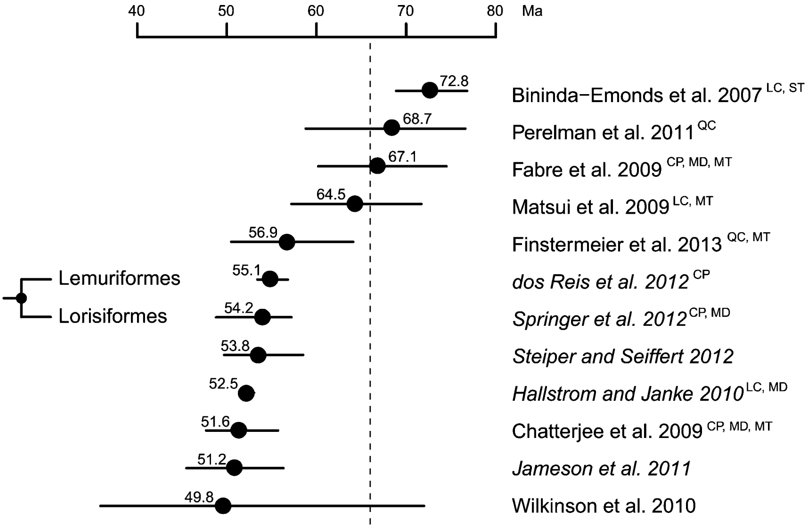

Fig. 9 Crown strepsirhine divergence date estimates. Abbreviations and italics as described in the caption to Fig. 2

Relationships of the Lemuriform Families

There are five families of lemurs: Cheirogaleidae (dwarf lemurs, mouse lemurs, and fork-crowned lemurs), Daubentoniidae (the aye-aye), Indriidae (indri, sifakas, and woolly lemurs), Lemuridae (true lemurs, ring-tailed lemur, ruffed lemurs, and bamboo lemurs), and Lepilemuridae (sportive lemurs). The sole point of agreement in higher level lemur systematics is that *Daubentonia* is the sister group to the others (Horvath et al. 2008; Chatterjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; McLain et al. 2012; Springer et al. 2012; Finstermeier et al. 2013; Masters et al. 2013; Yoder 2013). For the remaining four lemur families, there are four different topologies across the most recent lemur-focused or primate-wide phylogenetic studies (Fig. 10).

A sister group relationship of Cheirogaleidae and Lepilemuridae receives support across most studies (Fig. 10a–c) (Horvath et al. 2008; Chatterjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; McLain et al. 2012; Springer et al. 2012; Masters et al. 2013). The sole study that did not recover a Cheirogaleidae-Lepilemuridae clade has quite limited taxon sampling among the lemurs, is based only on the analysis of mtDNA sequences, shows a unique Indriidae-Lepilemuridae clade (with very low bootstrap support), and estimates divergence dates on a tree different from their best fit tree (dated tree has a Indriidae-Lemuridae clade) (Finstermeier et al. 2013).

Of the studies that do report a cheirogaleid-lepilemurid clade, two alternate topologies for the relations of the Indriidae and Lemuridae receive notable support. First, three studies report that the indriids are the sister taxon to the

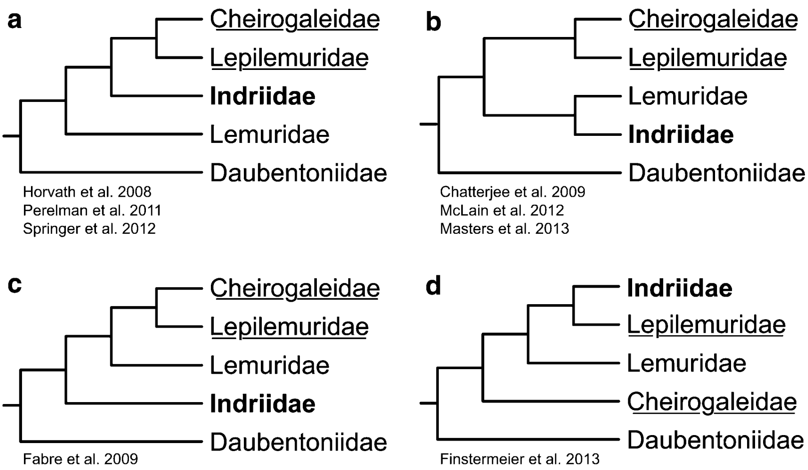

Fig. 10 Alternate hypotheses of relationships within the lemuriforms. Four different topologies for the branching relationships among the Cheirogaleidae, Indriidae, Lemuridae, and Lepilemuridae have been proposed in recent molecular systematic studies. The major difference among these cladograms is the position of the Indriidae (in *bold*). Most hypotheses of relationship have the Cheirogaleidae and Lepilemuridae as sister taxa (these families are *underlined*)

cheirogaleid-lepilemurid clade (Fig. 10a) (Horvath et al. 2008; Perelman et al. 2011; Springer et al. 2012). However, these studies do not constitute independent confirmation of this relationship. Perelman et al. (2011) include the 11 loci developed by Horvath et al. (2008) in their 54-locus data matrix, and Springer et al. (2012) add an additional 15 sequences to the Perelman et al. data matrix. In addition, all report poor bootstrap support for the node grouping the indriids with the cheirogaleid-lepilemurid clade. Second, three other studies report an Indriidae-Lemuridae clade as the sister group to the cheirogaleid-lepilemurid clade (Fig. 8b) (Chatterjee et al. 2009; McLain et al. 2012; Masters et al. 2013), but without strong support. Masters et al. (2013) and Chatterjee et al. (2009) both analyzed mtDNA sequences and report bootstrap support of 50 % or less for the indriid-lemurid clade. McLain et al. (2012) identified 111 new transposable elements informative for lemur phylogeny but did not find any additional support for a indriid-lemurid clade beyond the single transposable element insertion previously reported by Roos et al. (2004). While homoplasy by convergence (independent, identical insertion or perfect excision) is unlikely for transposable elements (Ray et al. 2006), they are no more immune from homoplasy by incomplete lineage sorting or secondary admixture than any other genetic marker (Churakov et al. 2009).

Divergence Dates Within the Lemuriforms

Because there are no fossil lemurs, fossil-calibrated divergence date estimates for the lemur radiation are probably less reliable than estimates of other primate divergence dates. The lineage leading to *Daubentonia* is estimated to have diverged from the other lemurs between 45 and 60 Ma, with most falling between 45 and 50 Ma (Fig. 11a) (Bininda-Emonds et al. 2007; Chatterjee et al. 2009; Fabre et al. 2009; Matsui et al. 2009; Perelman et al. 2011; Springer et al. 2012; Finstermeier et al. 2013; Masters et al. 2013). The split of the cheirogaleids and the lepilemurids is estimated to have occurred between 27 and 33 Ma (Fig. 11c) (Horvath et al. 2008; Chatterjee et al. 2009; Perelman et al. 2011; Springer et al. 2012; Masters et al. 2013).

Divergence dates among the other lemur families will be difficult to pin down while the phylogeny remains in flux. For instance, for those studies that reported a cheirogaleid-lepilemurid clade, their estimates of the time of divergence of this clade from their closest relative are shown in Fig. 11b. For this node, a trichotomous divergence of the cheirogaleids, the indriids, and the lepilemurids is estimated at 31 Ma (Springer et al. 2012), the divergence of the cheirogaleid-lepilemurid clade from a indriid-lemurid clade is found to be between 32 and 34 Ma (Chatterjee et al. 2009; Masters et al. 2013), and the divergence of the cheirogaleid-lepilemurid clade from the indriids is estimated at 35–38 Ma (Horvath et al. 2008; Perelman et al. 2011). While it is tempting to read the differences in divergence dates for this node across the different phylogenetic reconstructions as informative, this impulse should probably be resisted. The Perelman et al. dates are generally on the higher end of the range of estimated dates, particularly for the deeper nodes, and the

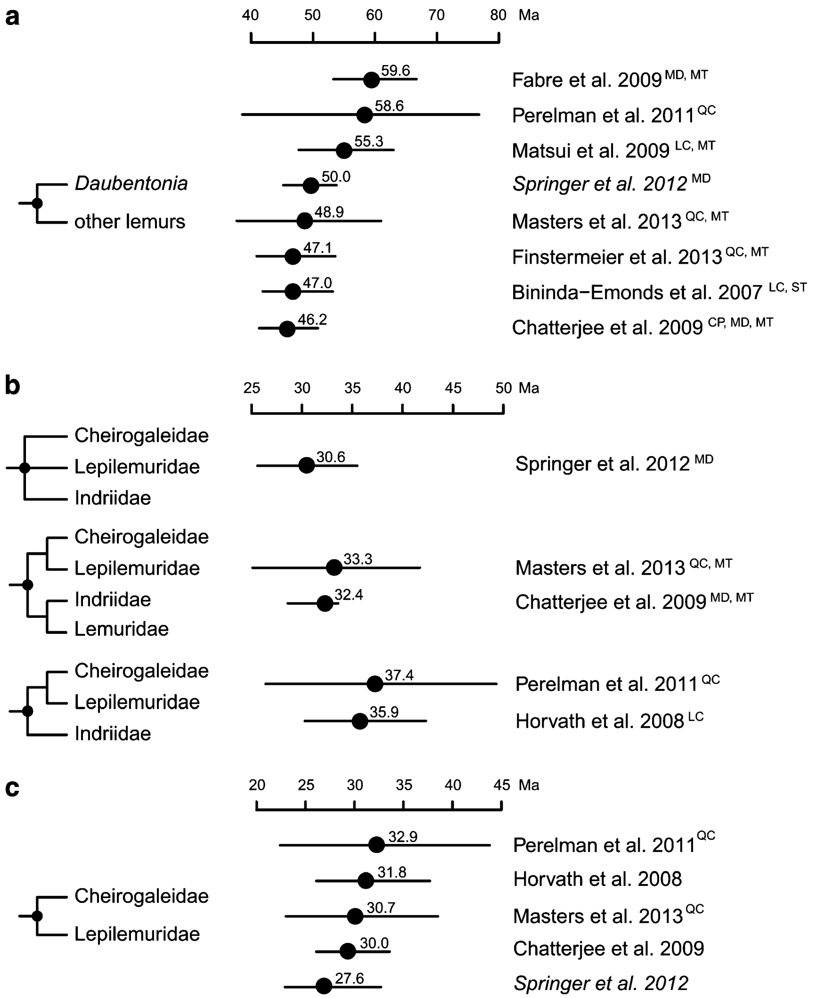

Fig. 11 Divergence date estimates among lemuriform families. Abbreviations and italics as described in the caption to Fig. 2

Springer et al. dates are usually more recent (see Figs. 2, 3, 4 and 9). The best that can be said at the moment is that the diversification of the non-*Daubentonia* lemur lineages probably began in the early Oligocene or late Eocene.

Relationships Among the Galagos and Lorises

Traditionally, Lorisiformes are split into two families, the African Galagidae (galagos or bush babies) and the African and Asian Lorisidae (lorises, slow lorises, and pottos). Each of these families has a host of apparently shared, derived behavioral, physiological, and osteological features confirming their monophyly (Rasmussen and Nekaris 1998). However, almost all early molecular studies suggested that the lorises are paraphyletic, with one or more genera more closely related to galagos than to the other lorises (Porter et al. 1997; Goodman et al. 1998; Yoder et al. 2001).

More recent studies based mostly or entirely on mtDNA sequence analysis continue to recover loris paraphyly (Chatterjee et al. 2009; Fabre et al. 2009; Matsui et al. 2009; Finstermeier et al. 2013; Masters et al. 2013), while those based on sequences from multiple nDNA loci recover loris monophyly, with the Asian Lorisinae (*Loris* and *Nycticebus*) sister to the African Perodicticinae (*Arctocebus* and *Perodicticus*) (Perelman et al. 2011; Springer et al. 2012). Transposable element insertions support the division of the lorises into these African and Asian clades but do not resolve a trichotomy among the galagos, African lorises, and Asian lorises (Roos et al. 2004). The combination of the extensive phenotypic data linking the lorises with the molecular confirmation of this group in studies based on nDNA is good evidence for loris monophyly. However, the molecular data alone are not convincing. The three nDNA sequence-based studies reporting loris monophyly are based on intersecting data matrices and report poor bootstrap support for the node linking the lorises (Horvath et al. 2008; Perelman et al. 2011; Springer et al. 2012).

Divergence Dates Within the Lorisiforms

Estimates for the minimum time of divergence between the Lorisidae and Galagidae range from 34 to 41 Ma (Bininda-Emonds et al. 2007; Perelman et al. 2011; Springer et al. 2012). The subsequence divergence of the Asian and African lorisids may have taken place within 3 Ma or less of this basal diversification. If this short internode time between the basal lorisiform and the basal lorisid split is correct, it would explain the difficulty that has been encountered resolving this node with molecular data. With short times between divergences, not only do fewer shared, derived mutations develop, but incomplete lineage sorting is more likely (Degnan and Rosenberg 2009).

A Galagidae-Lorisidae divergence at 35 Ma (Springer et al. 2012) would appear to conflict with evidence from the fossil record, where the earliest crown lorisiforms are dated at 37 Ma (Seiffert 2007), but it must be remembered that fossil-calibrated divergence dates estimate the most recent possible date of divergence. The Galagidae-Lorisidae divergence is very commonly used as a calibration point (Table 1), based on the identification of the late Eocene *Karanisia* as a lorisid and the similarly late Eocene *Saharagalago* as a galagid (Seiffert et al. 2003; Seiffert 2007). While Springer et al. (2012) did set a lower bound for the Galagidae-Lorisidae divergence at 37.1 Ma, they also used soft-bounded calibration points as part of their estimate, which allow date estimates outside of the calibration bounds. Assuming the dating of the deposits is correct, later studies should consider setting a harder lower boundary for this calibration point.

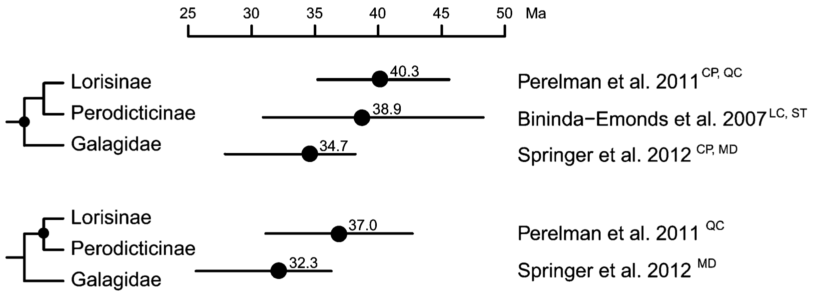

Fig. 12 Divergence date estimates among lorisiform families. Abbreviations and italics as described in the caption to Fig. 2

Future Directions

Beyond the division between the lorisiforms and the lemuriforms and the division of the lemuriforms between *Daubentonia* and all other lemurs, none of the interfamilial relations of the strepsirhines are completely resolved. There is some intriguing evidence that both the lorisiform families and most of the lemuriform families diversified rather rapidly in the latest Oligocene and earliest Miocene (Figs. 11 and 12) that deserves further study and better resolution of the divergence date estimates. Better resolution of these divergence dates is complicated, especially in the lemuriforms, by the absence of a fossil record for calibration. Even the mostly calibration-free method of Steiper and Seiffert (2012) requires phenotypic information from fossils to best model changes in evolutionary rate through time.

Conclusion

Many questions in higher level primate systematics now have good answers. Unless overwhelming evidence and convincing analysis can be presented that the tarsier is actually more closely related to the strepsirhines, anyone who mentions the haplorhine affinities of the tarsier as an important result of their study reveals only that they have nothing interesting to say. The relationships among the platyrrhine families are now well resolved in favor of a sister group relationship between the Cebidae and the Atelidae. Molecular evidence is beginning to converge on the monophyly of the lorises long found in morphological analyses. On the other hand, there are still many questions without completely convincing answers, including the branching pattern among the primates, colugos, and treeshrews; the relationships among the (non-Daubentoniidae) lemur families; and the placement of *Aotus* within the Cebidae. Most of these should be resolvable with more extensive genome-wide data from the relevant taxa.

Divergence date estimates are still in flux, especially in the depths of the primate radiation. For these questions, more genome-wide data from the relevant taxa is certainly going to be helpful, but methodological developments are going to be more important. Beyond the discrepancy between how we would like to interpret these dates (as the time of lineage divergence) and what they actually are (the most recent possible date of lineage divergence), there is also the problem of poor precision. Confidence intervals on divergence date estimates are broad, often encompassing millions of years, even for relatively recent nodes, and it may be that current methods cannot achieve greater precision (Schrago and Voloch 2013). New methods that attempt to directly estimate molecular evolution rates with little to no reliance on fossil calibrations offer some hope that it might be possible to produce divergence date estimates that can be interpreted as actual lineage divergences (Langergraber et al. 2012; Steiper and Seiffert 2012). For these methods to be successful, it will be necessary to carefully quantify the relationship between characteristics measurable in the fossil record (i.e., body size) and life history characteristics related to variation in the rate of molecular evolution (i.e., generation time). In this, we will need help from our colleagues in primatology, especially since many compilations of primate life history data appear to be undependable (Borries et al. 2013).

Many questions also remain in genus- and species-level primate systematics. First, there is the question of identifying all extant primate species. New species are still being described (Hart et al. 2012), and ongoing, and perhaps ultimately fruitless, debates on delineation of identified populations into distinct species continue (Jolly 1993; Weisrock et al. 2010). In addition, relationships among the genera within many families and relationships among species within genera remain unresolved in many cases. Some of the difficulties that are encountered in addressing these lower level phylogenetic questions are consequences of limited data and will be easily resolved by whoever is able to obtain sequences from multiple independent nDNA loci for the group in question. However, many of these problems seem to be the result of mismatches among gene trees and between many gene trees and the species tree as a result of incomplete lineage sorting and secondary hybridization and introgression (Tosi et al. 2003; Detwiler 2004; Burrell et al. 2009; Roos et al. 2011; Wall et al. 2013). Resolving those relationships will be complicated and could shed light on some of the difficulties encountered in resolving higher level relationships of primates.

Cross-References

- ▶ Ancient DNA
- ▶ Fossil Record of the Primates from the Paleocene to the Oligocene
- ▶ Genetics and Paleoanthropology
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Patterns of Diversification and Extinction
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence

▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
▶ Quantitative Approaches to Phylogenetics
▶ Species Concepts and Speciation: Facts and Fantasies

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Fossil Record of the Primates from the Paleocene to the Oligocene

Marc Godinot

Contents

M. Godinot (✉)
Ecole Pratique des Hautes Etudes and Muséum National d’Histoire Naturelle, Paris, France
e-mail: godinot@mnhn.fr

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Abstract

The Paleogene primate fossil record is reviewed following higher systematic categories. Among Strepsirhini, Adapiformes underwent Eocene radiations in North America (Notharctinae) and Europe (Cercamoniinae, Adapinae). Several occasional occurrences due to dispersals are found in North America, Europe, and Africa. Asia reveals a limited diversification (Sivaladapidae) and isolated occurrences indicating a central yet poorly understood role. In Africa the origin of living Lemuriformes is documented in the Late Eocene; odd stem lemuriforms occur earlier. The Eocene florescence of Omomyiformes is documented in North America (Anaptomorphinae, Omomyinae) and in Europe (Microchoeridae). Isolated occurrences, including the stem genus *Teilhardina*, are known in Asia. Two genera of Tarsiidae, known in the Middle Eocene of Asia, lead to a possible character-based definition of Haplorhini. The Asiatic Eosimiidae may belong in this group, and *Archicebus* may possibly lie on its stem. The Eocene South Asiatic Amphipithecidae are specialized hard-object feeders whose affinities remain enigmatic. Character-based Anthropoidea, or Simiiformes, are documented in the Late Eocene and Oligocene of Africa (Parapithecidae, Proteopithecidae, Oligopithecidae, Propliopithecidae). Toward the end of the Oligocene, the first African proconsuloids and the first South American platyrrhines appear. Anthropoidean origins are still a field of debate and discovery, with unconvincing Asiatic stem simians and a possible role for African Afrotarsiidae. The fossil record is extremely uneven, going from richly documented lineages in the Eocene of North America, to well-delineated radiations in the Eocene of North America and Europe and the Eocene–Oligocene of Africa, to more dispersed occurrences and enormous gaps during the early periods in Africa and Asia. The latters explain persisting controversies. Many aspects of primate evolution are documented over almost 20 million years, including locomotion, diet, vision and other sensory capacities, brain evolution, and one aspect of social structure via sexual dimorphism. The best records allow researchers to approach specific lineages, evolutionary modes, and analysis of faunistic changes.

Introduction

When Ludwig Rütimeyer (1862) referred some dental remains from the Swiss locality Egerkingen to an Eocene primate, his contemporaries did not believe that this was possible. Othniel Marsh later recognized primates through some lemur-like limb bones from the Eocene of Wyoming. When skulls with complete postorbital bars were found in the Quercy phosphate quarries in 1873, the scientific community had to admit that lemur-like primates had inhabited North America and Europe in Eocene times, and that *Adapis*, named much earlier by Georges Cuvier from a partial and crushed skull, was indeed a primate. Since then the discoveries have continued; indeed, so many have been added in the last decades that there are now more than 250 species of fossil primates known between the Late Paleocene and the end of the Oligocene. The record also includes families of Plesiadapiformes that are excluded here (see below).

The Paleogene is the first period of the Tertiary sub-era. It comprises three successive Epochs: the Paleocene, Eocene, and Oligocene. It starts at the famous Cretaceous-Tertiary (K-T) boundary, a geological limit around 65 million years ago ("Ma" will be used in the text for million years ago, and "My" for million-year durations). This limit coincides with an extinction event which affected many groups in the ocean and on land, including the then-dominant dinosaurs. These extinctions allowed the explosive diversification of mammals, among them the primates. However, not all groups of mammals are recognizable in the Early Paleocene. Several modern orders of mammals are well known only 10 Ma later, in the Eocene. Such is the case for primates, despite one exception in the Late Paleocene. Geological epochs, the main stages, some geological formations, stratigraphic scales, and some of the most important localities are shown in Fig. 1.

The Order Primates can be defined by a series of derived characters shared by all living members of the order: presence of a postorbital bar (or complete postorbital septum) surrounding large eyes that are directed forward and allow some degree of stereoscopic vision; presence of a maximum of two incisors, indicating loss of one incisor relative to primitive eutherians; a tympanic bulla formed by the petrosal; presence of an opposable hallux (prehensile foot) and typically presence of nails instead of claws (the two living primate groups bearing claws – Callitrichinae among South American monkeys and *Daubentonia* among Malagasy lemuriforms – are considered to have secondarily evolved claws from a nailed ancestor). These synapomorphies allow a clear delineation of living primates from all other mammals, including tree shrews, which between the 1920s and 1980s were usually considered to be primitive primates. This same definition excludes the Paleocene-Eocene Plesiadapiformes, which lack a postorbital bar and large forward-directed eyes, and also bear claws. If another more inclusive definition of primates is used, subsuming the plesiadapiforms, the above criteria apply at a lower systematic level, defining Euprimates as opposed to Plesiadapiformes (see chapter "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence," Vol. 2).

The origin of the primates as defined above is still undocumented, because terrestrial faunas from the right time and region are lacking. A dense and continuous fossil record of mammals is known in North America, but primates originated

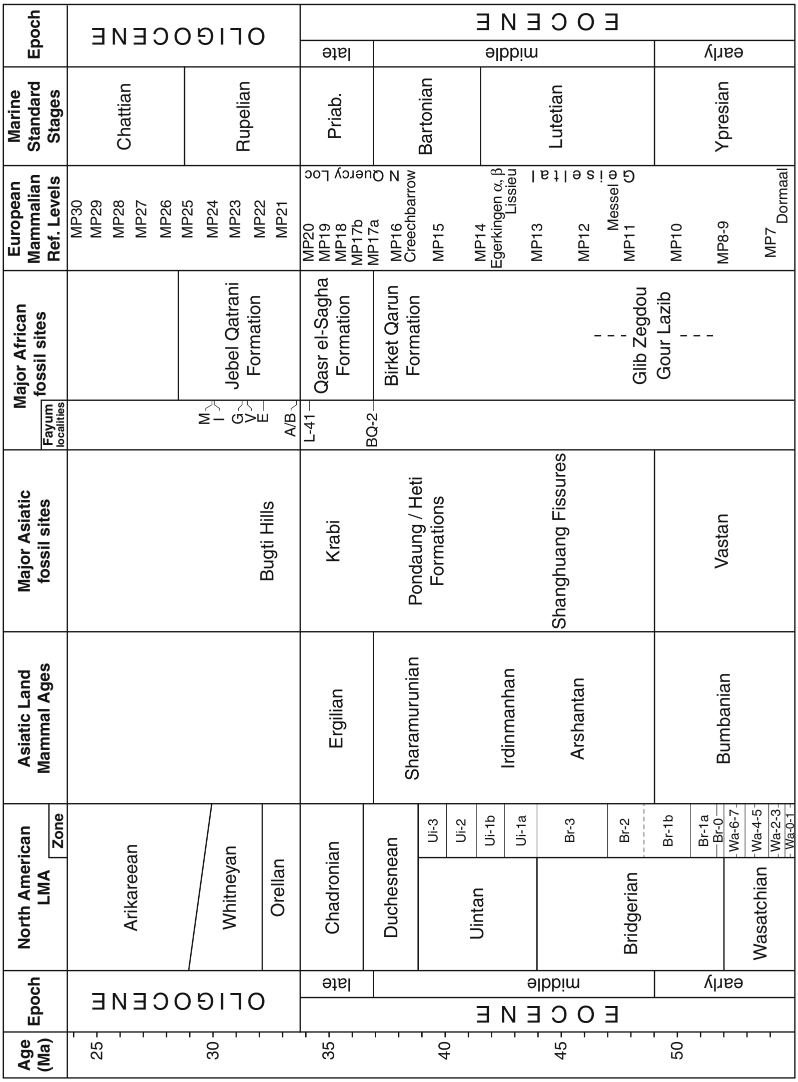

Fig. 1 (continued)

elsewhere. A more discontinuous fossil record of Paleocene mammals is known in South America, in Europe, and in Eastern Asia (Mongolia, China), but again without early primates. Despite recent progress, the Paleocene fossil record of mammals remains very poor in Africa, although one fauna yielded the single Paleocene primate known at the moment, *Altiatlasius* from Morocco, discussed below. This fossil shows that primates had reached Africa by the Late Paleocene; however, there is strong evidence that they did not originate in Africa but rather in Asia, where their two living sister groups, the tree shrews and flying lemurs, are found today (see chapter "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence," Vol. 2). A Paleocene fossil record of Southeast or Western Asia should give some definitive clues to this enigma; it would at the same time test a competing scenario, that of an origin on the northward-rafting Indian plate.

The Paleocene-Eocene boundary, 55 Ma ago, witnessed a series of climatic and paleogeographic events that resulted in the first occurrence of primates in North America, Europe, and Asia (China). This occurrence is part of a much broader dispersal event concerning several orders of mammals as well as other animals and plants. This dispersal followed a dramatic episode of global warming, which is one of the most fascinating climatic events discovered in the last 20 years (e.g., Aubry et al. 1998). Starting in the Early Eocene, a tropical climate and environment at high latitudes allowed the radiation of primate groups on northern continents, including Europe and North America. For geological and historical reasons, these radiations have been the best documented, allowing the study of well-circumscribed primate radiations during almost 20 My. However, these relatively well-known groups became extinct around the Eocene-Oligocene boundary, close to 33 Ma. The latter is marked by a global climatic cooling, rendering northern continents inhospitable for primates. Therefore, these Eocene radiations shed no light on the origin of living primate families, the history of which took place in Asia or on southern continents. This explains why, despite a rich Eocene fossil record, there are still controversies concerning the origin of major groups of living primates, among them the anthropoids: they originated in regions and times with a still insufficient fossil record. The northern Eocene radiations also increase the complexity of primate systematics and phylogeny. The phylogeny inferred from living primates is consensual. It divides them into two suborders: the Strepsirhini, which include the Lemuriformes (Malagasy lemuroids and Afro-Asiatic lorisoids), and the Haplorhini, which unite Anthropoidea or Simiiformes with extant Tarsiidae. The introduction of a variety of fossil families renders these notions problematic, as will be seen below. The term "prosimians" will also be used, to designate all non-anthropoidean primates.

◄

Fig. 1 Summary chart showing ages, epochs, marine standard stages, and mammal ages or reference-levels for terrestrial deposits on different continents. Some of the main localities or formations containing primates are indicated. Ma is for millions of years, LMA is for land mammal ages, and Ref. Levels is for the European mammalian reference-levels (MP). The North American Wasatchian is recalibrated following recent work on the Wasatchian-Bridgerian transition. The richest primate records are found in the best-documented intervals, especially the Early Eocene in North America, the Late Eocene in Europe (N Quercy Loc refers to the new Quercy localities), and the Eocene-Oligocene in North Africa (BQ2 to M refer to the Fayum fossil localities)

Because there are many uncertainties and debates in primate phylogeny, an important conceptual choice is made in this chapter: the adoption of character-based definitions of higher taxa. This choice serves both clarity and stability, as will become apparent on several occasions below. It is usually well recognized that a crown group definition of taxa (all species descended from the common ancestor of living forms) has inconveniences: if many members of a group are extinct, the crown group is too small. Williams and Kay (1995) illustrated this with examples like the genus *Homo*, which cannot be limited to *H. sapiens*. One might add that the well-known *Aegyptopithecus* is usually considered a catarrhine, although it probably does not pertain to the crown group. Concerning the order Primates, a character-based definition is provided above. There might be several clades bearing the five primate synapomorphies listed above which would be branches preceding the strepsirhine/haplorhine dichotomy. It would not be reasonable to exclude such groups from the order Primates because they branch before the dichotomy leading to the living groups. Different but equally unfortunate inconveniences arise from the use of stem-based definitions. Too often, the node separating two higher taxon stem lineages is unknown, so that fossils can be moved from one higher taxon to another and back, depending on cladistic analyses whose results often appear highly unstable. And if the node were known, i.e., the genus in which the initial speciation took place, stem-based definitions would lead to a spread between different higher taxa of species of one and the same stem genus. Any such definition of a higher taxon becomes minuscule in terms of characters, i.e., almost useless. All these inconveniences, bound up with definitions that proceed either from living in-group survivors or from living sister groups, are avoided by the use of character-based definitions. Furthermore, in primate origins and in primate evolution, a number of important anatomical innovations occurred, and instrumental use of these in systematics helps to convey this critical information, instead of ignoring it.

The fossil record is presented here via the well-documented major radiations since the Early Eocene: Adapiformes and Omomyiformes, followed by their close kin Lemuriformes and Tarsiiformes, respectively. Several enigmatic groups are mentioned next, before Simiiformes (=Anthropoidea) and anthropoidean origins are discussed. The following rough size categories will be used: “very small” for primates weighing 100 g or less, “small” for primates between 100 and 500 g, “middle-sized” for primates between 500 g and 2 kg, and “large” above 2 kg. Weight is a very important adaptive and ecological factor; however, the estimation of body weight in fossils is not easy. Body weight estimates will be given only for fossils for which weight indications from dental remains can be supplemented by estimates based on cranial or postcranial remains.

The Adapiformes Radiations

The Adapiformes are an almost cosmopolitan group of fossil primates which diversified during the Eocene and survived in Asia until the Late Miocene. They include around 46 genera and 105 species. They provide some of the best-known fossil primates. In terms of size, dental adaptation, and locomotion, they compare relatively closely with living lemurs. Hence they are usually described as lemur-like, and some cranial and postcranial characters seem to justify their grouping with living Lemuriformes as strepsirhines, a notion analyzed below.

The Adapiformes divide into three families: the Notharctidae, Adapidae and Sivaladapidae.

North American Notharctids

The Notharctidae are the oldest documented adapiforms, being represented in the Earliest Eocene by the genus *Cantius* in North America and Europe, and by the genus *Donrussellia* in Europe only. From these two stem genera, two subfamilies diversify: the Notharctinae mainly in North America (plus *Cantius* surviving several My in Europe), and the Cercamoniinae in Europe. In North America, the history of the subfamily is well known. There are around 10 species of *Cantius* in North America. The oldest, *C. torresi* and *C. ralstoni*, as well as the European *C. eppsi*, show the typical dental characters of the genus (Fig. 2). The dentition is on the whole moderately bunodont, having somewhat rounded molar cusps. Small incisors, a large canine, and four premolars are typical primitive primate characters. P/1 to P/3 are simple, with one main cusp increasing in size and the posterior part broadening from P/1 to P/3. P/4 is still longer, has a well-formed metaconid, and a broad and short talonid with a small median hypoconid cusp. The lower molars increase in length from M/1 to M/3, whereas the trigonid becomes anteroposteriorly shorter. There is a large lingual paraconid well separated from the metaconid on M/1, and the paraconid merges progressively with the metaconid summit on M/2 and M/3. The trigonid is transversely broad and opens posteriorly on M/3, which is typical of *Cantius* and advanced over *Donrussellia*. M/3 has an elongated third lobe, and its triangular outline, narrowing posteriorly, is also typical of the genus. P3/ and P4/ have massive outlines. The protocone lobe is slightly narrower than the labial part on P4/, and much narrower and smaller on P3/. The M2/ is always more transversely elongated than M1/, which is slightly anteroposteriorly longer. Both have small conules, a postmetaconule-crista going toward the base of the metacone, and a distinct protocone fold.

A lineage *Cantius–Notharctus* is documented in the Bighorn Basin of Wyoming by successive assemblages that can be placed in a synthetic stratigraphic sequence. The assemblages are so close in time and in morphology that this provides one of the most convincing cases of gradual evolution in mammals (Gingerich 1976). This lineage includes the successive species *C. ralstoni, C. mckennai, C. trigonodus, C. abditus*, and *C. nunienus*. These species have no precise boundaries, but the distinction between them is necessary to convey the underlying evolutionary information. The lineage is characterized not only by the size increase evident on diagrams, but also by the progressive development of new dental characters, including an entoconid notch on the lower molars, a hypocone on the upper molars, as well as a mesostyle which will progressively lead to W-shaped labial crests as found in several living folivorous primates (Gingerich and Simons 1977). The hypocone

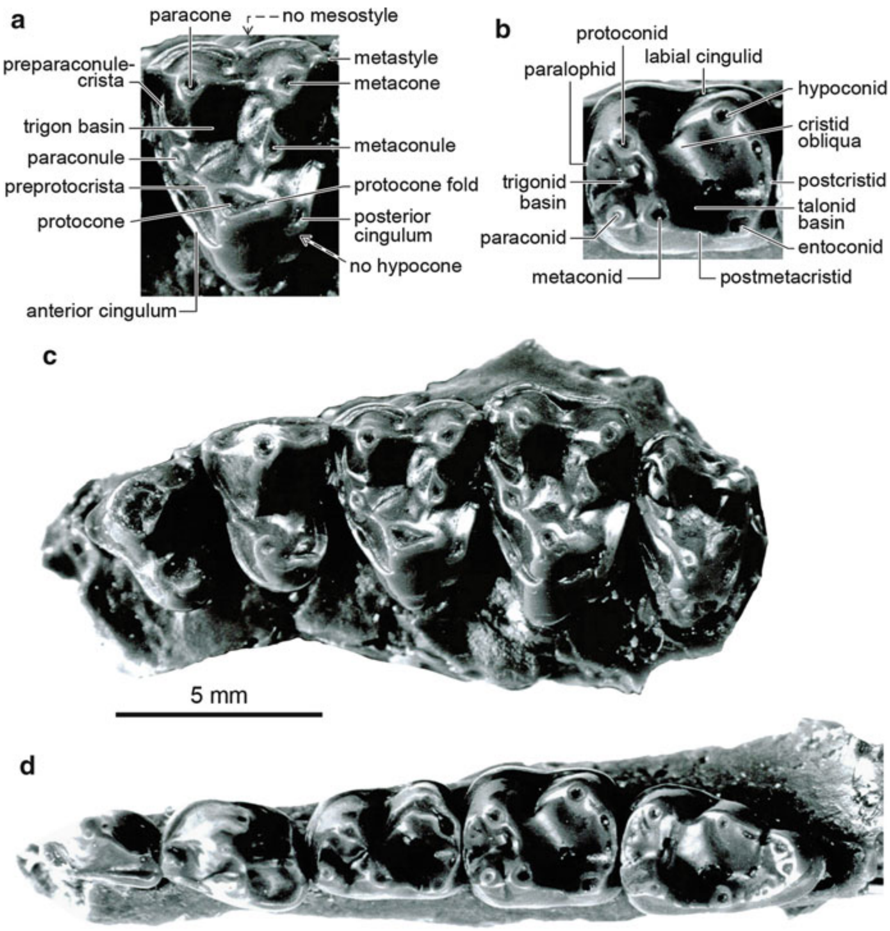

Fig. 2 Upper and lower jugal teeth of *Cantius eppsi* showing the primitive dental morphology of notharctines. (**c**), upper series from P3/ to M3/; (**d**) lower series from P/3 to M/3. The upper M1/ in (**a**) and the lower M/2 in (**b**) illustrate most of the terms of dental morphology used in the text. Upper molars have three main cusps and no hypocone. Lower M/1 and M/2 have large paraconids, and P/4 has a main cusp and is relatively elongated (photographs of epoxy casts)

grows on the protocone fold, not from the cingulum as in most other primates. It is thus often referred to as a pseudohypocone. *Cantius* had unfused lower jaws, anteriorly appressed; some later *Notharctus* have frequently fused lower jaws, with a long horizontal symphysis. Variations in the size and orientation of the anterior lower incisors among *Cantius* and *Notharctus* species are illustrated by Rose et al. (1999). The lineage keeps four premolars all along. Among other species, *C. simonsi* is the largest one, found in Late Wasatchian beds (Wa7) of the Bighorn basin; *C. angulatus* is found in the San Juan Basin of New Mexico; and *C. frugivorus* is found in the latter and in several other basins (Beard 1988; Gunnell 2002).

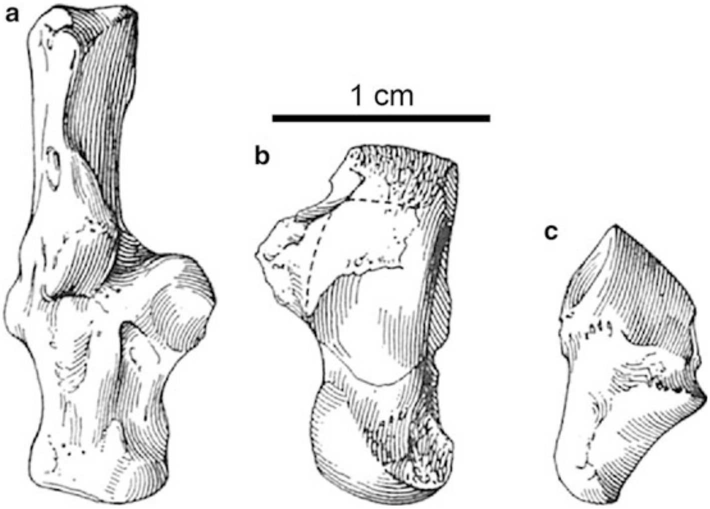

Fig. 3 Foot bones of *Cantius frugivorus*. (**a**) calcaneum; (**b**) astragalus; (**c**) entocuneiform; all in dorsal view. The distal articulation of the entocuneiform for the first metatarsal is sellar in relation to the opposability of the first pedal digit (hallux) typical of primates (From Matthew in Matthew and Granger 1915)

A crushed skull of *Cantius abditus* appears relatively short and broad in its proportions. It displays characters that are interpreted as primitive in notharctids, such as a ventrally keeled basioccipital, a flat basisphenoid, and proximally broadening nasals (Rose et al. 1999). The auditory region is very similar to that of *Notharctus* and living lemurs. It shows a large stapedial artery and a much smaller promontory artery, which seems to have followed an open sulcus along the promontorium. This morphology, shared with lemurs, may be primitive in adapiforms, and the bony tubes present in *Notharctus* and *Smilodectes* may be derived.

A partial skeleton of *Cantius trigonodus* includes a fragment of a distal humerus with a prominent brachialis flange, a proximal ulna with a well-developed olecranon process, and a proximal and distal radius showing a strong shaft (Rose and Walker 1985). A partial pelvis shows a relatively long ischium and short ilium compared with living lemurs, probably primitive. The femoral head is less spherical than in living lemurs, and relatively far separated from the greater trochanter. The distum of the femur is anteroposteriorly high, with a prominent lateral ridge, suggesting leaping abilities. The proximal tibia shows retroflexed condyles and a prominent tibial crest. The relatively distal tibial tuberosity may indicate quadrupedalism and also be primitive, associated with the long ischium. An astragalus, a calcaneum and an entocuneiform of *C. trigonodus* were figured by Matthew in Matthew and Granger (1915) (Fig. 3). Adding characters of the astragalus and the prominent peroneal tubercle of a proximal hallucial metatarsal, Rose and Walker (1985) infer for *Cantius* the locomotor behavior of an active arboreal quadruped with a propensity for leaping. Additional foot bones, cuboid, navicular, medial cuneiform, and a distal nail-bearing phalanx of *C. mckennai* were

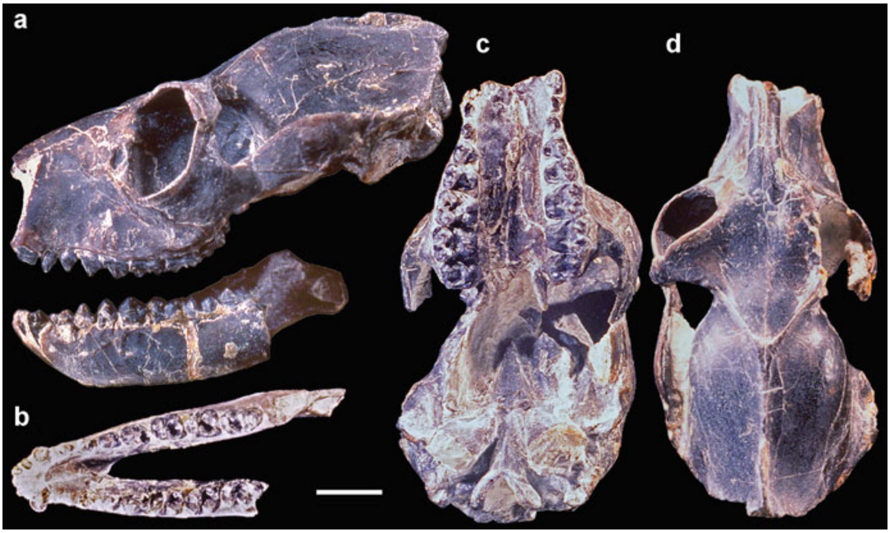

Fig. 4 Skull of *Notharctus tenebrosus* in profile view (**a**), mandibles in occlusal view (**b**), and cranium in ventral (**c**) and dorsal (**d**) views. The dorsal view shows some deformation of the left zygomatic arcade, which may have a slightly exaggerated orbit height on the profile view. The mandibles have a long, inclined, fused symphysis

described by Covert (1988), who inferred high foot mobility and powerful grasping in this species. Because tarsals are frequently found in general and the Early Eocene fossil record is rich, more than 150 tarsals of *Cantius* species, and probably some *Pelycodus* and *Copelemur*, were identified (Gebo et al. 1991). They show no significant change, whereas there are some small differences between them and later *Notharctus* and *Smilodectes* tarsals.

Species of *Notharctus* became particularly well known with the publication of a beautiful monograph by Gregory (1920). The reconstruction of the skull of *N. tenebrosus* by Gregory, based on distorted specimens, was not exact from today's perspective, with too long a muzzle. This has since been corrected due to the discovery of more complete skulls (Alexander 1994; Godinot 1998), which show a higher and shorter muzzle (Fig. 4). Partial skeletons allowed Gregory (1920) to describe long bones, a partial scapula and pelvis, and foot and hand bones. He could conclude the analysis of *Notharctus*'s locomotor behavior by inferring a clear leaping adaptation, albeit one less extreme than in living vertical clingers and leapers (VCL): in *Notharctus* the forearm still played a more important role in locomotion, muscular insertions on the pelvis were less pronounced, and feet were less specialized than in living indriids. More recent studies have generally concurred with Gregory, with nuances emphasizing either *Notharctus*'s leaping propensity or, in contrast, its quadrupedal postures. It can be viewed as a frequent leaper, though probably a pronograde (horizontal) leaper and quadruped rather than a VCL. Gregory had reconstructed an incomplete and very long hand. A more complete specimen allowed the description of all carpals, metacarpals, and phalanges, and a better reconstruction of the hand

(Hamrick and Alexander 1996). This hand has remarkably long digits due to very long proximal phalanges. The thumb is divergent, and the short second metacarpal appears markedly divergent from the third. The second digit is reconstructed unreduced and placed in the middle of the space between digits one and three. This results in a functionally bizarre hand, which furthermore bears a strange and unique distal phalanx on the second digit. The divergence of the metacarpals and length of the digits give rise to the suspicion that this hand might have used schizodactylous grips, with the support between digits two and three as in living *Alouatta*.

There are five species of *Notharctus*. *N. venticolus* is the earliest one, known from the latest Wasatchian and earliest Bridgerian, and in temporal and morphological continuity with *Cantius abditus*. An assemblage of this species has clearly shown a strong sexual dimorphism in upper canine size and shape, as admitted by earlier authors from more scattered specimens (Krishtalka et al. 1990). The species is followed by *N. robinsoni* (BR1B) and *N. tenebrosus* (BR2). Skull shape differences between males and females in *N. tenebrosus* have been described by Alexander (1994), and beautiful skull illustrations have been produced (Alexander and Burger 2001). *N. robustior* is the largest species of the genus, which had a body weight estimated between 6 and 8 kg.

Another well-known Middle Eocene genus is *Smilodectes*. The best-known species is *S. gracilis* (Middle Bridgerian), whose skull and endocranial cast were described by Gazin (1958, 1965). It has a slightly shorter and higher cranium than *Notharctus*. Its skeleton is also well known, but was not studied in as much detail as that of *Notharctus*. The two are in fact broadly similar. *Smilodectes* too had a pronograde and leaping adaptation. It also developed the shearing adaptation of the upper molars (W of labial crests), which produced similar upper molar characters. Such similarities can result in the two genera appearing as sister groups in a cladistic analysis (Covert 1990). However, *Smilodectes* has a long ventrolingually sloping paralophid on the lower molars, which indicates a different lineage, not derivable from *C. trigonodus*, and convergence with *Notharctus* in upper molar characters. The same result is obtained after careful evaluation of the characters sustaining different trees obtained by cladistic analysis, leading researchers to favor the close relationship of *Smilodectes* and *Copelemur* – included in a tribe Copelemurini — and as a consequence postulating convergences between *Smilodectes* and *Notharctus* (Beard 1988; Gunnell 2002). There are two other species of *Smilodectes* besides *S. gracilis*: *S. mcgrewi* is Early Bridgerian, and *S. sororis* is earliest Bridgerian, both of Wyoming.

Species of *Copelemur* are characterized by low and anteroposteriorly elongated P/2–4, lower molars with narrow trigonids, a small ventrally placed paraconid or paralophid, and an anteriorly shifted entoconid linked to the trigonid by a long postmetacristid and followed by an entoconid notch; upper molars have a mesostyle, and a protocone fold but no hypocone (Gingerich and Simons 1977; Beard 1988). There are three species of *Copelemur*, starting with *C. praetutus* from the Middle and Late Wasatchian (Wa4-6) of Wyoming and Colorado. It is followed by *C. australotutus* (Wa5-6) and *C. tutus* (Wa7), the latter of which was the first discovered, by Cope, in the San Juan Basin of New Mexico. *Copelemur* is considered closely related to *Smilodectes*; however, the origin of neither taxon is clear, probably involving southern and less well-sampled regions.

Two other genera are recognized in the North American Eocene, *Pelycodus* and *Hesperolemur*. *Pelycodus* is more bunodont than other notharctines. *P. jarrovii* is found in the late Wasatchian (Wa6) of New Mexico and rarely shows up in Wyoming. *P. danielsae*, known only by two fragmentary specimens, is a very large species with an estimated weight of above 6 kg (Froehlich and Lucas 1991). The origin of *Pelycodus* probably lay in the poorly documented southern regions of the United States. A rooting in the earliest Wasatchian *Cantius torresi* seems possible. The case of *Hesperolemur* is more complex. It was named based on a cranium and two other specimens from the Uintan of California (Gunnell 1995b), but the interpretation of some of its cranial characters was later criticized by Rose et al. (1999), who proposed to refer it to a species of *Cantius*. However, it differs from the most derived species of *Cantius* and appears somewhat reminiscent of *Pelycodus*, albeit distinct from it due to its weak mesostyle. Gunnell (2002) still considers it to be a valid genus. North American notharctines became extinct in Wyoming at the end of the Bridgerian, but *Hesperolemur* found refuge in Southern California in the Early Uintan. Their extinction is related to the shrinking of forested areas, due to the surrection of the Rocky Mountain Range and drying of the areas on its eastern side.

European Notharctids

The European notharctid radiation also starts in the Earliest Eocene, represented by a primitive species of *Cantius*, with survivors during the Early Eocene, and by species of *Donrussellia*, more primitive than *Cantius*, that seem to be at the root of the European Cercamoniinae. *D. provincialis* from Rians, southern France, shows the most primitive adapiform dentition known today (Fig. 5). The anterior part of the dentary is thin and presents a very anteriorly inclined symphyseal region. Alveoli suggest small incisors (probably two), a large canine, a single-rooted P/1, and a double-rooted P/2. P/3 and P/4 are elongated and narrow, P/4 bears an incipient metaconid. A slight crowding of the premolars is shown by some inclination of the roots of P/2 and P/3, the anterior one being more labial than the posterior one. M/1 has a big lingual paraconid well separated from the metaconid; its trigonid is longer than its talonid. The trigonid of the lower molars decreases in size from M/1 to M/3, the paraconid becoming smaller and closer to the metaconid. The talonid basin, in contrast, increases from M/1 to M/3, which has a relatively expanded third lobe. The upper molars are transverse and simple, without any trace of lingual cingulum or hypocone. The postprotocrista starts with a short posterior inclination, being continuous on M2/ and interrupted on some M1/, but there is no real protocone fold. The conules are small and there is no postmetaconule-crista. Other species of *Donrussellia* are known: *D. lusitanica* in Silveirinha, Portugal (Estravis 2000), the small and more insectivore-like *D. gallica* from Avenay, Paris Basin, and the larger *D. magna* from Palette, southern France, which appears

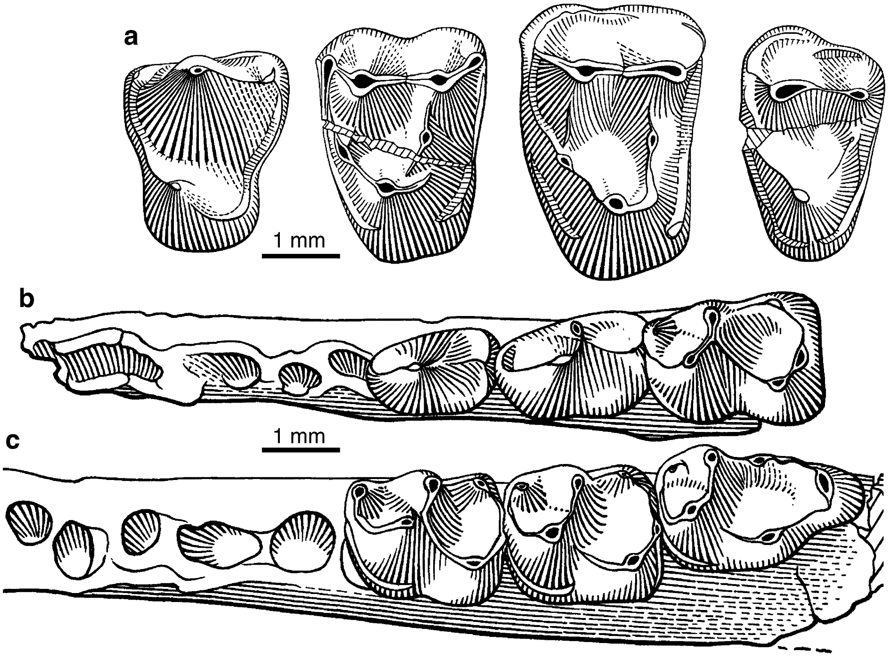

Fig. 5 Dentition of *Donrussellia provincialis*. Upper teeth, P4/ to M3/ (**a**), one mandible showing P/3 to M/1 (**b**), and one with M/1 to M/3 (**c**). The *upper* teeth are among the most primitive known in primates, with three main cusps and no hypocone. Lower molars also show a primitive large trigonid on M/1-2 with a well-formed paraconid. P/3 and P/4 are simple and relatively narrow. Alveoli reveal a relatively large canine followed by a single-rooted P/1 and a double-rooted P/2

intermediate with *Cantius* and thus suggests that at least three species dispersed into Europe in the Earliest Eocene.

In the late Early Eocene, larger and more derived species occur, which can be associated in groups of related genera. The first group includes *Protoadapis, Europolemur*, and *Barnesia*. Species of *Protoadapis* appear less common now than previously thought. The earliest species seems to be *P. curvicuspidens*, named long ago by Lemoine from late Early Eocene sites which are not precisely located. The species is present but rare in Grauves, the MP 10 reference locality. In *Protoadapis*, the paraconid is a residual cuspule on a relatively long and subhorizontal paralophid. The genus is also characterized by a P/3 higher than P/4. Other similar-sized species of *Protoadapis* are *P. angustidens*, from an unknown level in the Quercy, and *P. ignoratus* and *P. muechelnensis*, from the Middle Eocene lignite mines of the Geiseltal, Germany (MP 12, Thalmann 1994). Two larger species of *Protoadapis* are also described from lower jaws alone. *P. (Cercamonius) brachyrhynchus* is also from an unknown level of the Quercy fissure fillings, whereas *P. weigelti* is from the same level in the Geiseltal as the above-mentioned species. These species have more robust teeth and jaws. Robustness of the jaw and possible anterior premolar reduction and more vertical symphysis led Gingerich (1975) to erect the new genus *"Cercamonius"* for the species *brachyrhynchus*, considered to be evolving toward anthropoid characters. However, Thalmann (1994) followed Szalay and Delson (1979) in rejecting the new genus, noting only small differences between *P. brachyrhynchus* and *P. weigelti*. More material is necessary to ascertain the differences between these species, and *Cercamonius* can be retained as a subgenus to mark its distinctness. Species of *Protoadapis* remain poorly known, with only a few upper teeth referred to *P. curvicuspidens*, among which one figured specimen is misidentified (Russell et al. 1967).

Species of *Europolemur* are known through partial skeletons found in the Middle Eocene localities of Messel and the Geiseltal in Germany, and dental material from Eckfeld, Bouxwiller, and probably also the Paris Basin in France. The Messel Oil Shale deposited in a volcanic lake dated close to 47 Ma. The skeleton of *Europolemur koenigswaldi* was found there in two parts: the anterior part, crushed skull, forelimb, and trunk were found first (Franzen 1987); the rear part was found later, allowing the reconstruction of the entire animal (Franzen and Frey 1993). It was relatively small. The first weight estimate from dental regressions was close to 2 kg; however, a more reliable estimate from trunk length suggests a much lower weight, around 300 g, underlining the uncertainties associated with weight estimates from tooth dimensions alone. Crushed skeletal parts are difficult to study, but they show parts that are most often unknown in fossils. The anterior part is that of a young adult, with erupting M/3 and still functional DP/3–4/. The muzzle appears elongated, and the small orbits suggest a diurnal way of life. Incisors are in place, recalling those of *Notharctus*, with I1/ two times broader than I2/. From the breakage not being in midline, Franzen (1987) deduced that the two mandibles were fused. X-ray images show the outline of middle ear ossicles within the right tympanic bulla, as well as parts of a tympanic ring. The vertebral column is preserved from the axis to the os sacrum, the latter consisting only of two fused sacral vertebrae. Ribs 1–13 can be seen. A right forearm is there, from scapula to hand. The scapula, rarely found in fossils, has a shape close to that of *Galago* and *Eulemur macaco*. The broad humerus is broken. The hand shows flexed digits, digit one isolated from the others on the palmar side, as well as a large pisiform. Two distal phalanges appear broad, flat, and scutiform. The rear part of another individual, ascribed to the same species, shows a long tail with 30 vertebrae. Proportions of femur and tibia led to a crural index of 83, and an estimation of the intermembral index of 72.6. Among the tarsals, the astragalus shows a wedge-shaped trochlea, and a neck and a posterior trochlear shelf more extended than in *Notharctus*. The calcaneum is slender, elongated (index of anterior part 45.2 %), and with a short posterior astragalar facet – characters which suggest leaping propensities. The two feet are complete but crushed. Their metatarsals are short, the first one being very robust. The terminal phalanges are quite narrow with a flat plantar side, suggesting the presence of narrow nails (this difference with the anterior part is bizarre, raising a question about their association). There is no special toilet claw. Franzen and Frey (1993) reconstruct *E. koenigswaldi* as an arboreal quadruped, climbing above branches and having leaping capacities.

Another somewhat larger species is *E. kelleri*, named from a crushed skull. Several earlier finds were referred to this species: a pelvis, baculum, and hindlimbs, and a forearm with hand (Franzen 1988, 2000a; von Koenigswald 1979). *E. klatti* from the Geiseltal is the type species of the genus. It was described from a crushed cranium bei Weigelt (1933). Its dentition includes a large laterally compressed upper canine, a small P2/ and a single-cusped P3/, upper molars with complete lingual cingulum and large hypocone, but no metaconule. Details on the variation in dental characters are given by Thalmann (1994), who tentatively ascribed to the species some isolated postcranials, an atlas, an astragalus, and a calcaneum. *E. dunaifi* from Bouxwiller, known only through isolated teeth, appears very close to *E. klatti*. A crushed cranium from the highest level of the Geiseltal (MP 14) shows upper teeth close to those of *Europolemur*, though different enough for Thalmann (1994) to erect a new genus and species, *Barnesia hauboldi*. Its M2/ is enlarged in comparison with M1/ and M3/. It is transversely elongated, and on its lingual cingulum a pericone is added to a moderately large-sized hypocone. The species is possibly present in Bouxwiller.

The genera *Pronycticebus* and *Godinotia* constitute an isolated lineage rooted in primitive forms. It has been known for a long time through the description by Grandidier (1904) of a beautiful cranium and jaw coming from the old phosphate exploitations of the Quercy region, southern France, which he named *P. gaudryi*. Its age is not precisely known; however, one tooth attributed to a close species was found in a new Quercy locality, dated MP 10–11. This suggests that *Pronycticebus* is probably a Lutetian genus. The skull of *P. gaudryi* is important because it is the only cercamoniine skull that is three-dimensionally well preserved. Its tympanic bulla and basicranial foramina are similar to those of lemurs and adapids, and partial preparation of one bulla also shows a free tympanic ring, which is often considered typical of strepsirhines (Le Gros Clark 1934; Simons 1962). A CT-scan analysis revealed the morphology of its bony labyrinth (cochlea and semi-circular canals), which appears closest to that of Adapinae, both having similarities with lemuroids (Lebrun et al. 2012). A relatively complete and somewhat crushed skeleton from an MP 12 level in the Geiseltal lignite series, Germany, was described as “*P.*” *neglectus* (Thalmann et al. 1989). A mandible previously ascribed to *Europolemur klatti* was also referred to this species by Thalmann (1994). The species was made the type of a new genus *Godinotia* by Franzen (2000b); however, this was based on the misallocation to this species of the first slab of *Darwinius* (see below). The species seems to be dentally close to *P. gaudryi*, but it differs from it by the loss of P1 and reduction of P2, which are single-rooted above and below, versus double-rooted in *P. gaudryi*. This may justify a generic (or subgeneric) distinction. Among the best preserved skeletal elements are a left humerus, a right forearm and hand, with some carpals, five metacarpals, and some very elongated proximal phalanges (Thalmann 1994). *Godinotia* appears to have more gracile limb bones than *Europolemur* and *Darwinius* (Franzen et al. 2009).

A third group of cercamoniines consists of *Agerinia*, *Periconodon*, and *Darwinius*. New faunas under study reveal an abundant new species in the Paris Basin that is close to *Agerinia* and *Periconodon*, and also appears closely related to *Darwinius* (Herbomel and Godinot 2011). Species of *Periconodon* are named after the presence of a supplementary cusp on the upper molars called a pericone (Stehlin 1916). The taxonomy is uncertain and provisionally follows Godinot (1988), with *P. helveticus* from Egerkingen as type species of the genus (Stehlin 1916). Its type specimen is a maxilla bearing P3/ and M1–2/. These molars have a transversely short trigon basin, a long lingual slope of the protocone, a well-developed pericone that is lingual or slightly anterolingual to the protocone summit, and a large hypocone. P3/ is high and pointed. Its lingual border is underlined by a moderate bulging, without any cusp or protocone lobe. A very close species is *P. huerzeleri* from Bouxwiller, the type specimen of which is a mandible (Gingerich 1977a). The lower molars of this species show a high intraspecific variability, e.g., M/1 with or without a tiny paraconid; lower molars with a clear separation between the premetacristid and the curved paralophid, or a paralophid continuous until the metaconid on M/3; and M/3 with a more or less extended talonid basin, with or without distinct entoconid. Upper molars vary in their transverse extension, and in the variable presence of a crest linking hypocone and pericone (Godinot 1988). Similar high variations occur on the teeth of *P. jaegeri* from a lower level at Bouxwiller, with hypocone and pericone varying from small to very large and lingually bulging. This species is typified by crenulated enamel and lower molars with a supplementary anterolingual crest issued from the metaconid (entometacristid). *P. helleri* is known through a maxilla from the Geiseltal series (MP 13–14). Its teeth are worn and chemically eroded. It shows a P4/ having a relatively short protocone lobe. A dentary of *Periconodon* sp. is reported from the rich locality Eckfeld Maar (MP 13). It preserves P/4, P/3, an incomplete and apparently two-rooted P/2, and the alveolus for a P/1 (Franzen 2004). The older *P. lemoinei* proposed by Gingerich (1977a) needs further study. Until now, all species of *Periconodon* are known dentally only.

Agerinia is known through its type species *A. roselli* from Les Saleres, Spain (MP 10), and through another species from southern France. Only lower teeth have been described, which include narrow P/3 and P/4 with curved preprotocristid and lingual cingulum. The lower molars have no more paraconid, and a paralophid joining a premetacristid, thus realizing a complete crest anteriorly joining protoconid and metaconid. The included trigonid basin (or fovea) becomes anteroposteriorly shorter and labiolingually longer from M/1 to M/3. The talonid basin is especially broad, with rounded outline, on M/1 and M/2. It is this distinctive morphology of M/2, with very short trigonid and broad talonid, which makes *Darwinius* remarkably similar to *Agerinia* in these rare derived traits. This suggests a close phylogenetic relationship between them, also shared with a new species from the Paris Basin (Herbomel and Godinot 2011).

D. masillae is the name given to the most complete Messel skeleton, which has an unusual history. After it was found by amateurs in the form of two opposite slabs, the first of these, which was incomplete, was supplemented by fake parts and described for the first time as the sixth Messel primate by Franzen (1994). It was at that time referred to "*Caenopithecus neglectus*." The preserved parts were

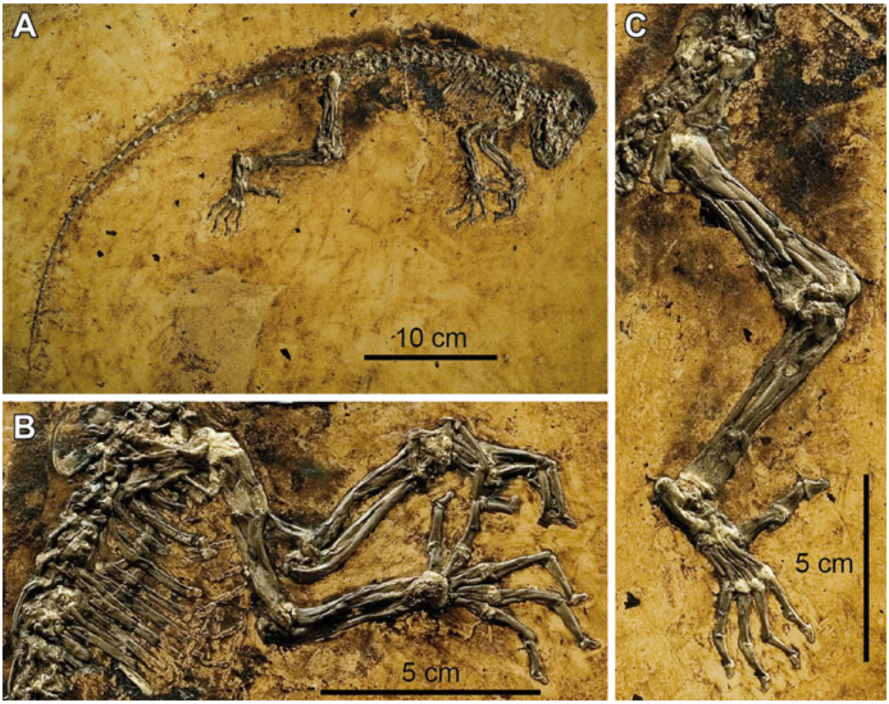

Fig. 6 The skeleton of *Darwinius masillae* from Messel, Germany. (**a**) the best-preserved plate; (**b**) detail of the same showing forelimbs and part of the vertebral column and rib cage; (**c**) detail of right hindlimb with complete foot. Note the presence of fur impressions on the complete skeleton, heavily crushed skull, a callus on the right wrist due to reaction after an accident, probably falling from a tree. The right foot shows a strongly opposable first toe and the dorsal side of the astragalus (Courtesy of J. L. Franzen)

already remarkable, including a crushed skull, the anterior part of the trunk and forelimbs up to the middle of the forearms, the rear part of the trunk, anterior part of the tail, and a hindlimb almost to the extremity of tibia and fibula. Outlines of the soft part of the body were visible. The specimen was described in detail. It is a juvenile individual with milk dentition and just erupted M/1, with a reduced DP/2, a short cranium, large orbits, and proportions of humerus, ulna, and tibia different from those of *Europolemur*. Further dental comparisons led Franzen to refer the species to a new genus as *"Godinotia neglecta"* (Franzen 2000b). Study of the dark remnants corresponding to gut content allowed the identification of a 3–4 mm seed coat and scattered leaf particles. These, together with the absence of insect cuticle, which is normally well preserved in insectivorous Messel mammals, suggest that the species had a frugivorous-folivorous diet (Franzen and Wilde 2003). Several years later, the second slab from the same individual was made available to science, leading to the in-depth analysis of the most complete fossil primate skeleton, now referred to *Darwinius* as *D. masillae* (Franzen et al. 2009) and nicknamed "Ida" (Fig. 6).

The complete skeleton confirms *Darwinius* to have possessed a relatively short rostrum, a steep face, large orbits, and a rather large braincase. Among its noticeable characters are the unusually short forelimb, the proximally curved ulna, mesaxonic hand (third ray the longest, primitive) with relatively small and short pollex, short metacarpals and long proximal phalanges, and scutiform nail-bearing distal phalanges. Analysis of its tarsus appears insufficient. Franzen et al. (2009) write that the fibular facet of the astragalus would be steep as in primitive primates ("haplorhines" for them); however, their best figure (idem Fig. 10) seems to expose the astragalus in dorsal view, showing mainly its tibial trochlea. A short ribbon of fibular facet is insufficient to describe its slope. The other parts of the foot – navicular, cuneiforms, and enormous pollex – are lemur-like, and it would be very surprising to find them associated with a laterally primitive astragalus. The fibular facet is steep but strepsirhine-like in closely related species from the Paris Basin (Godinot et al. 2011). Future micro-CT-scan studies will complete the first analyses, which raise some questions (e.g., the articulations between trapezoid and MC-II, and hamate and MC-V, are said to be saddle-shaped, which is bizarre). A radiographic study added to the CT-scan revals the pattern of dental replacement in Ida. The specimen is a juvenile with fully erupted M1, M2 probably erupted but with incomplete roots, M3 not erupted, DP3 and DP4 functional. Comparison with living primates suggests rapid growth, similar to that of "medium fast" primates with a maximum life span of 12–20 years (Schultz 1960; Franzen et al. 2009). It suggests that Ida was a juvenile, weaned and independently feeding, which during its life suffered an accident causing a severe trauma of its right wrist, probably a fall from a tree (Franzen et al. 2012). Ida has no baculum, whereas this bone is large and conspicuous in some *Europolemur* rear skeletons interpreted as males (von Koenigswald 1979); so Ida probably is a female. Its weight is estimated at 650–900 g, depending on the estimators. Its locomotion is reconstructed from a multivariate analysis as quadrupedal without specialization for climbing or leaping. However, such multivariate approach is likely to be influenced by evolutionary trends (e.g., the long lumbar region is likely primitive). The intermembral index (IMI) is more directly linked to locomotor adaptation. The IMI calculated for *Darwinius* from its measurements is 63–64, relatively low, indicating that its locomotion included frequent leaping. It is thus more likely to have been an arboreal quadruped leaper. A haplorhine status has been advocated for *Darwinius*, but only on weak grounds (Franzen et al. 2009). For example, a fused mandibular symphysis evolved many times in primates; loss of a grooming claw is uncertain in *Darwinius* but such a grooming claw exists in *Europolemur* and, moreover, reveals a complex pattern of evolution (von Koenigswald et al. 2012; Maiolino et al. 2012); see above concerning the fibular facet of the astragalus. *Darwinius* is a cercamoniine showing similarities with *Pronycticebus* (large orbit, large upper canine), as well as with *Agerinia* and *Periconodon* in dental morphology, and the placement of adapiforms with the strepsirhines appears well founded (see below).

A series of smaller species and genera of cercamoniines are known, mainly dentally. They include three genera close to *Anchomomys*, which will be grouped in a restricted tribe Anchomomyini. They lived during a large part of the Middle

Eocene. The smallest of them is the type species of *Anchomomys*, *A. gaillardi*, known by a maxilla and a mandible from Lissieu (MP 14), described by Stehlin (1916). The upper teeth are very simple, lingually narrow with the three main cusps, a continuous crista obliqua without metaconule, a paraconule, a very small incipient hypocone on M1–2/, and a non-reduced M3/. The lower molars are elongated and narrow. Typical of *Anchomomys* species is their almost rectilinear anterior paralophid, which in occlusal and in anterior view is at a roughly right angle with the strongly sloping preprotocristid. There is no trace of a paraconid. This thin paralophid, always well separated from the base of the metaconid, is reminiscent of adapines (and of *Pronycticebus* M/3). The trigonid becomes shorter from M/1 to M/3. Two dentaries from Egerkingen referred to *A.* cf *pygmaeus* (taxonomy uncertain) add some information. One shows a P/4 which is anteroposteriorly elongated, narrow, has no trace of a metaconid, and bears only one posterior median crest descending from the protoconid summit, and a well-formed talonid with hypoconid and lingually inclined basin surrounded by a lingual cingulid. The other dentary shows anterior alveoli, which suggest the presence of two small incisors, a relatively large canine, and a two-rooted P/2 (Stehlin 1916; Szalay and Delson 1979).

Other species of *Anchomomys* include the slightly larger *A. (Huerzeleris) quercyi*, which has a larger but still small hypocone. The type specimen is from old Quercy collections, without precise location; however, very close specimens have been found in new Quercy faunas from reference levels 16 and 17a. *A. frontanyensis* from Sant Jaume de Frontanyà (MP 14/15, Spain) completes our knowledge of the genus. Described are a robust, slightly recurved upper canine, small P1/, P2/, and larger P3/ which are subtriangular in outline, surrounded by an almost continuous cingulum. P4/ is transversely elongated with a well-formed protocone. M1–2/ have very small cingular hypocones (Marigo et al. 2011). Among the lower teeth are a robust canine with cingulids descending from the apex, a surprisingly large P/1 (P/2?), P/2, and P/3 oval in outline and surrounded by a continuous cingulid, and an elongated P/4 close to that of *A.* cf *pygmaeus*. Among the lower molars, several M/3 show an unusually high variability of their talonids, broad and short or elongated, with variable supplementary cuspules on their periphery. Postcranials of this species are known and allow a weight estimate of 120 g. The astragalus is close to those of small notharctids (Moyà-Solà and Köhler 1993). The first metatarsal has a moderate-sized peroneal process (Roig and Moyà-Solà 2011). The calcaneum has remarkable proportions. Its anterior part is more elongated than in any other known adapiform, rather resembling omomyids in this proportion. However, the authors conclude that such proportions are a compensatory effect in grasping foot postures, and not an indication of leaping propensities (Moyà-Solà et al. 2012). Other postcranials are said to confirm a cheirogaleid-like, generalized type of arboreal locomotion for *A. frontanyensis*.

Among the species closely related to *Anchomomys* are two species of *Buxella*, *B. prisca* and *B. magna*, described from the locality of Bouxwiller and known only by isolated teeth (Godinot 1988); *Nievesia sossisensis* from Sossis, Spain, known by a maxilla with M2–3/ and isolated teeth, is distinct due to the presence on the lower molars of a premetacristid joining the paralophid, closing a sloping trigonid

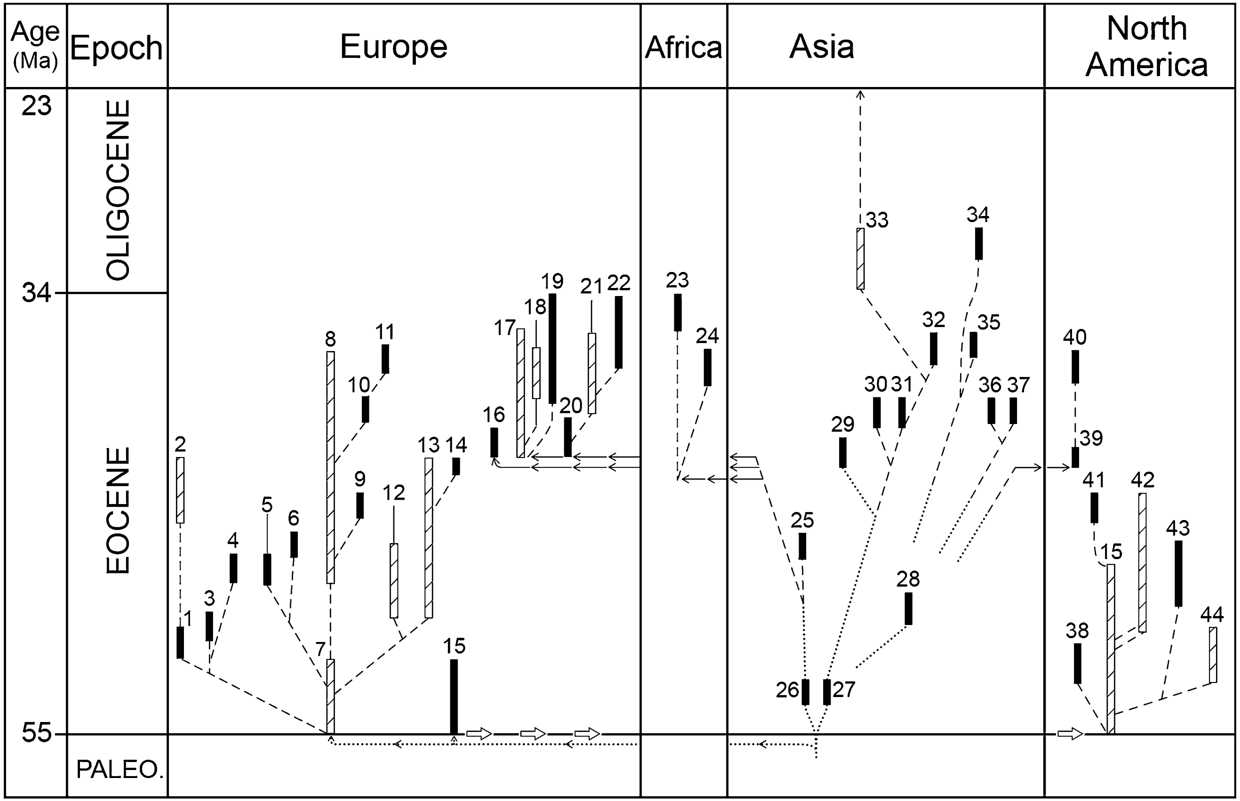

Fig. 7 (continued)

basin (Marigo et al. 2013); and *Mazateronodon endemicus*. The latter is from the Middle Eocene Spanish locality Mazateron (MP 15–16), in the Almazan Basin. This basin is further west in comparion with other Pyrenean/Catalan basins, and its fauna, including *Mazateronodon*, reveals some endemism relative to other European localities (Marigo et al. 2010). Like *Nievesia*, *M. endemicus* has lower molars with a closed trigonid basin. Two upper incisors referred to this species show an elongated cutting edge reminiscent of adapines. In contrast, a referred lower incisor seems not to fit well with the uppers and would suggest a great amount of evolution in comparison with the alveoli of *A.* cf *pygmaeus*. A referred P4/ has a very narrow lingual lobe. One mandible fragment with P/3–4 and the canine shows the latter to be robust and of triangular outline. P/3 and P/4 on this specimen and on another one are noteworthy: elongated, blade-like, slightly crowded with the anterior root more labial than the posterior one. P/3 is longer and higher than P/4, somewhat posterodorsally inclined; P/3 is slightly narrower, more elongated and more inclined on the specimen bearing the canine than on the other. On both, P/3 displays a long anterior blade, suggesting a possible honing mechanism for the robust upper canine (which is also described). This should be explored: it would be remarkable for such a small species. In any case, *M. endemicus* shows an interesting evolution of the lower premolars, possibly convergent with catarrhines. Middle Eocene anchomomyins survived longer than other cercamoniines, probably because their small size induced them to avoid competition with the then-dominating adapines. They must have been partly insectivorous.

Adapids in Europe and Three Other Continents

The family Adapidae is known by a classical group of European forms, the Adapinae, and by a series of more primitive and almost cosmopolitan forms (Fig. 7), provisionally grouped in the Caenopithecinae. The adapines arrive as

Fig. 7 Known stratigraphic ranges and suggested phylogenetic relationships among genera of Adapiformes. *Dashed bars* indicate genera including more than one specific lineage; *black bars* indicate that only one specific lineage is known; simple *vertical lines* indicate uncertainty in the stratigraphic range. The global picture of this record is a good reflection of the whole Eocene primate record: relatively well known in Europe and North America, much less in Africa. In Asia, which played a central role, several groups are documented; however, the record is too scanty to allow even a vague schema of possible relationships. *Dashed lines* indicate reasonable phylogenetic hypotheses; *dotted lines* indicate unknown origins and affinities for Asiatic groups. *Arrows* indicate dispersals between continents (or the continuation of sivaladapines in the Miocene above 33). *1*, new species close to *Periconodon* and *Agerinia*; *2*, *Periconodon*; *3*, *Agerinia*; *4*, *Darwinius*; *5*, *Pronycticebus*; *6*, *Godinotia*; *7*, *Donrussellia*; *8*, *Anchomomys*; *9*, *Buxella*; *10*, *Mazateronodon*; *11*, *Nievesia*; *12*, *Protoadapis*; *13*, *Europolemur*; *14*, *Barnesia*; *15*, *Cantius*; *16*, *Caenopithecus*; *17*, *Leptadapis*; *18*, *Magnadapis*; *19*, *Cryptadapis*; *20*, *Microadapis*; *21*, *Adapis*; *22*, *Paleolemur*; *23*, *Aframonius*; *24*, *Afradapis*; *25*, *Adapoides*; *26*, *Marcgodinotius*; *27*, *Asiadapis*; *28*, *Panobius*; *29*, *Lushius*; *30*, *Rencunius*; *31*, *Hoanghonius*; *32*, *Wailekia*; *33*, *Guangxilemur*; *34*, *Bugtilemur*; *35*, *Muangthanhinius*; *36*, *Paukkaungia*; *37*, *Kyitchaungia*; *38*, *Pelycodus*; *39*, *Mescalerolemur*; *40*, *Mahgarita*; *41*, *Hesperolemur*; *42*, *Notharctus*; *43*, *Smilodectes*; *44*, *Copelemur*

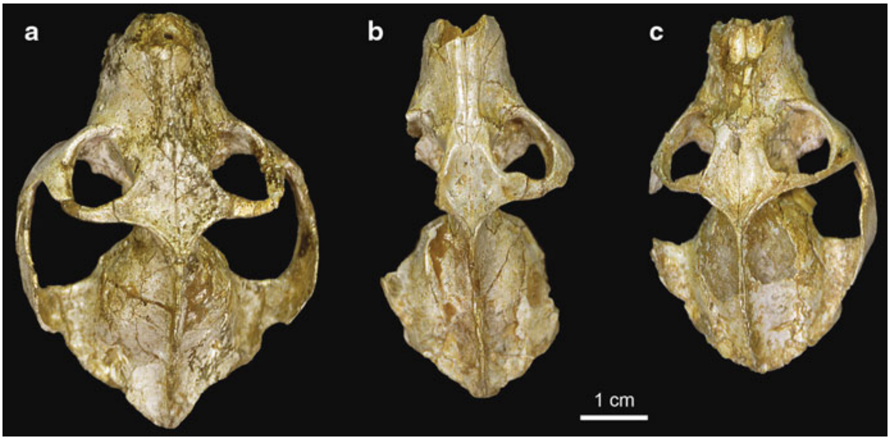

Fig. 8 Three crania of Late Eocene large adapines coming from old Quercy collections. (**a**) is the type specimen of *Magnadapis intermedius*, (**b**) is the type specimen of *Leptadapis magnus*, and (**c**) is the type specimen of *L. filholi*. Note that the interorbital breadth and the muzzle are larger in (**a**) than in (**b**) and (**c**). Cranial superstructures are also more developed in (**a**) in comparison with the two others; however, specimens with very low or no sagittal crest exist in both genera

several lineages, *Microadapis* and *Leptadapis* (including *Paradapis*), between reference levels 13 and 14. Until now, it has not been possible to root them convincingly in European cercamoniines, despite some similarities. Surprisingly, a species with marked similarities with adapids has been found in China, suggesting an origin of the subfamily in some intermediate area and strengthening the notion of a dispersal into Europe. Adapines make a small radiation in the Late Eocene of Europe, documented by the beautiful skulls found in the Quercy fissure fillings in the nineteenth century. A detailed description and analysis of these skulls was provided by Stehlin (1912). Information on one beautifully preserved cranium of *Adapis* and its endocast is given by Gingerich and Martin (1981). A careful revision of the large-sized adapines more recently has led to the distinction of two genera: *Leptadapis*, with a narrow interorbital breadth and muzzle (three species), and *Magnadapis*, with broader interorbital breadth and muzzle (four species) (Fig. 8). In both genera, some species show large or extreme cranial superstructures (sagittal and nuchal crests, thickened zygomatic arcades), while others show small ones or none. Whereas one study had proposed to interpret these differences as a marked sexual dimorphism (Gingerich 1981), restudy of more material, which underlined modest differences in canine sizes and morphological changes in dental morphology, led to the hypothesis of different lineages, some of them characterized now by a marked increase in cranial superstructures (Godinot and Couette 2008). A similar systematic revision is needed for the smaller *Adapis*-sized species, which are also numerous (Lanèque 1992, 1993). The postcranials of adapines are distinctive, showing no hindlimb lengthening and calcanea which have a very short anterior part, shorter than in any living strepsirhine (Dagosto 1983). The sole known complete femur has a relatively broad distal end (Fig. 9). These characters are

Fig. 9 Limb bones of *Adapis*-sized adapines from the old and new Quercy collections. The humerus (**a**), femur (**b**), and tibia (**c**) may come from the same fissure : They have the same type of preservation and were described together by Filhol. The calcaneum (**d**) and the first metatarsal (**g**) also come from old Quercy collections, whereas the two astragali come from two new localities, Rosières 2 (**e**) and Escamps (**f**). Proportions of humerus and femur suggest a not-elongated hind limb. The anterior part of the calcaneum is particularly short, and the peroneal tubercle of the first metatarsal is small. The two astragali are quite different, (**e**) with a much longer trochlea and (**f**) with a shorter, broader, and flatter one reflecting different locomotor adaptations in different *Adapis*-sized species

interpreted as indicative of climbing and a relatively slow locomotion (Dagosto 1983). However, some *Adapis*-sized species appear to have varied in locomotor modes, one being more walking and running than the other (Godinot 1992a; Fig. 9). The variety of femora that can be attributed to *Adapis*-sized species show that they underwent a diversification in their locomotor adaptations, resulting in five different types, some of which were more climbing and others more walking and running forms (Bacon and Godinot 1998).

All of these adapines have highly crested molars and molarized P/4. Their phylogeny is rather complex and not yet understood. Species of *Cryptadapis* had a large hypocone, whereas large adapines show a progressive reduction of this cusp. Several lineages further increase their shearing adaptation in developing a metastylid on their lower molars. They appear adapted to shearing food, which is suggestive of degrees of folivory; however, they varied in their diets. Microwear analysis suggests that *Cryptadapis tertius* was strictly folivorous, whereas one *Adapis* species added more fruits to its diet than two other adapines (Ramdarshan et al. 2011). Adapine remains from well-dated faunas reveal that the large genera, *Leptadapis* and *Magnadapis*, preceded the mid-sized ones, and that the latter became extinct in the Quercy region at the end of the Eocene. The adapines apparently did not survive the Terminal Eocene Event, or "Grande Coupure," in Europe, which involved an invasion of Asiatic mammals better adapted to more open environments, as well as to cooler and more seasonal climates. However, it seems that one species of a relatively large adapine briefly survived the dispersal event in England (Hooker 2010).

The more primitive adapids provisionally grouped in the subfamily Caenopithecinae are found in Europe, North America, Africa, and possibly Asia. The Asiatic *Adapoides troglodytes*, from the Middle Eocene Shanghuang fissure fillings, China, is known by a lower dentary with M/2–3 and isolated upper molars and DP4/ (Beard et al. 1994). Its lower molars are so derived in an adapid direction, with anteroposteriorly compressed trigonid, long ventrolingually sloping paracristid, and deep talonid notch, that they could point toward adapine affinities. However, the upper molars (including the "*Europolemur*-like" molar of Beard et al. 1994) are transversely elongated and show no hypocone or only a tiny incipient one, characters markedly more primitive than in the adapines. Without knowledge of the P4/4 and their degree of molarization, it will be difficult to determine the place of this genus relative to the adapines. A small adapiform astragalus from Shanghuang appears already adapine-like, suggesting climbing propensities (Gebo et al. 2001). The European primitive adapids include *Caenopithecus* and *Microadapis*, which arrive in Europe at the same time (Egerkingen fissure fillings, Middle Eocene, Switzerland). *C. lemuroides* shows a number of similarities with later adapines, but it also has non-molarized P/4/ –a primitive trait – and a metastylid on the lower molars and a mesostyle on the uppers, the latter being a derived character unknown in adapines and otherwise found, among adapids, only in the African *Afradapis*. *Microadapis* is small, has no metastylid, a simple premolariform P/4 and relatively narrow and elongated P/4–2, and a moderate-sized P/1. A referred upper molar bears a very large hypocone, as well as a metaconule – a small cusp usually lost in other genera, including *Adapoides*. The most primitive adapids probably differentiated somewhere on the Eurasiatic landmass between Europe and China. *Marcgodinotius* from India (see below) might have some relevance.

The two African genera *Aframonius* and *Afradapis* from the Late Eocene deposits of the Fayum, Egypt, also appear to show affinities with this group, revealing its dispersal into Africa. *Afradapis longicristatus* is from the Late Eocene BQ-2 locality (Seiffert et al. 2009), whereas *Aframonius dieides* is from the Latest Eocene locality L-41 (Simons et al. 1995; Simons and Miller 1997). The two genera have upper molars with a broad trigon basin, high crests, and a large hypocone linked to the posterior cingulum (Fig. 10). The long and sharp centrocrista is slightly labially deflected on the M2/ and M3/ of *Aframonius*, and even more

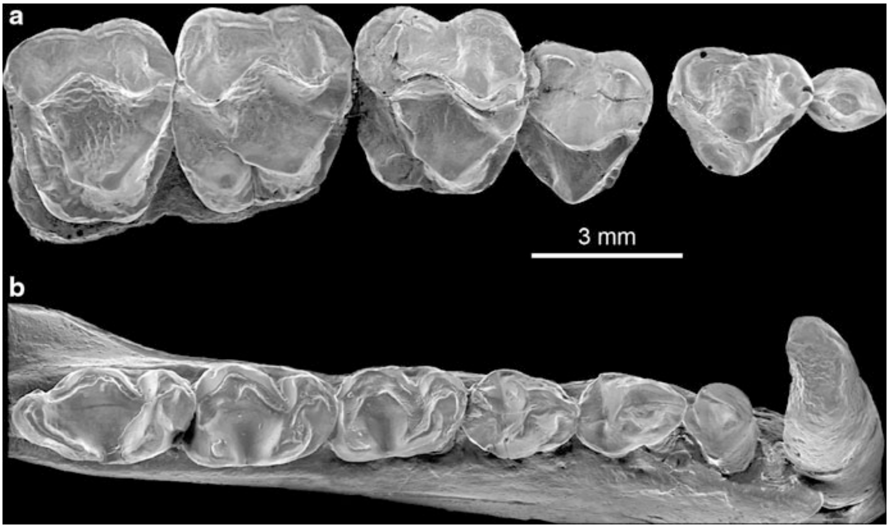

Fig. 10 The dentition of *Aframonius dieides* from the Fayum, Egypt. (**a**) upper dentition from the large M3/to the small P2/in occlusal view; P3/and P4/are in a more labial orientation, with the protocone partly hidden, due to specimen deformation; (**b**) lower dentition from M/3 to the lower canine in occlusal view. Scanning electron micrographs (SEM) of casts

deflected and joining a mesostyle on the M1–2/of *Afradapis*. Their P4/ are simple with a broad protocone lobe, and their P3/ are triangular due to a narrower protocone lobe. Both have lower molars without paraconids. Those of *Aframonius* have shorter paracristids, and metaconids posterior relative to the protoconid. Those of *Afradapis* have a more anterior metaconid, a longer protocristid, and longer paracristids which increasingly curve toward the metaconid summit from M/1 to M/3. The P/3–4 of *Aframonius* are relatively short, posteriorly broad, and only incipiently molarized. The P/3 and P/4 of *Afradapis* are remarkable and unique among adapiforms. P/4 is elongated, molarized through a high metaconid almost as anterior as the protoconid, has a well-formed and narrow talonid basin, and is unusual because of its anteriorly elongated protocristid. P/3 is even larger than P/4, higher and much longer. Its anteriorly elongated protocristid served as a honing device for the large upper canine. Lower dentaries show that there was no P/2 in *Afradapis*, which appears convergent with catarrhines in the possession of only two premolars and an enlarged P/3 honing with the upper canine. The dentaries of *Afradapis* were fused, whereas there was variability in this character in *Aframonius*, which retains a moderate-sized P/2. Both upper and lower isolated incisors have been ascribed to *Afradapis*. The lowers make a transverse cropping mechanism analogous to that of *Adapis*. A large phylogenetic analysis proposed a placement of the two African genera close to the European *Caenopithecus* (Seiffert et al. 2009). Given that *Aframonius* had some more primitive characters, the two groups likely share a close common ancestor, whose descendents were able to disperse to Europe and to North Africa in the Middle Eocene.

Finally, there are two North American genera, *Mahgarita* and *Mescalerolemur*, which are of uncertain affinities. *Mahgarita stevensi*, from the Latest Eocene of Texas, has long been recognized to have no affinity with the North American notharctines (Wilson and Szalay 1976). Similarities with primitive adapines led to its inclusion in that group (Godinot 1998). However, the description of the older and more primitive *Mescalerolemur horneri* and more detailed phylogenetic analyses showed the adapid features of *Mahgarita* to be probably convergent, and both these genera to be probably rooted in more primitive adapiforms (Kirk and Williams 2011). A dispersal from Asia, as for many other Eocene forms, appears likely. Both genera have upper molars with a well-formed crestiform hypocone and complete lingual cingulum on M1–2/. M2/ is transversely broader than M1/. The M1/ of *Mescalerolemur* is more triangular, with a strong prehypocone-crista and an expanded basin posterior to the postprotocrista. Whereas *Mahgarita* has a P4/ with a broad protocone recalling adapines, that of *Mescalerolemur* has a much narrower protocone lobe. P3/ is triangular, dissymmetrical due to its posterior protocone lobe, in *Mahgarita*. It is even more unusual in *Mescalerolemur*, with a pinched posterior protocone lobe underlined by a strong posterior ectoflexus. Both taxa have lost P1 and have reduced P2 above and below. The lower molars of both genera have very reduced paracristids. *Mescalerolemur* has a small anterior paraconid on M/1 only. The posteriorly broad and elongated M/3 of *Mahgarita* could be reminiscent of adapines; however, similar morphologies occur in cercamoniines as well, and *Mescalerolemur* has a shorter and posteriorly narrower M/3. P/3 and P/4 appear particularly simple in both genera, transversely narrow and with no metaconid or paraconid. In *Mahgarita*, where the large canines are known, the lower canine is posteriorly recurved, but the upper canine – straight, with a strong basal cingulum, a sharp posterior crest, and vertical grooves – is somewhat reminiscent of *Leptadapis*. *Mescalerolemur* has an unfused symphysis, whereas *Mahgarita* has a fused one – evidently one more convergence with adapines and with many other primates. These two genera have an overall similarity and very peculiar P3–4/ which demonstrate their close affinity. *Mescalerolemur* is lacking clear derived similarities with adapids, and its origin will be in more primitive Asiatic adapiforms.

The holotype of *Mahgarita stevensi* is a crushed cranium which shows a number of features: a high maxilla, a pronounced posterior palatal spine, a very low occipital height, and a posteriorly directed foramen magnum. The basicranial morphology was earlier considered essentially lemur-like (Wilson and Szalay 1976). Further study of this crushed cranium and two other partial crania led Rasmussen (1990) to add a number of observations. For example, there is noticeable petromastoid pneumatization; one specimen has a much reduced stapedial canal and the other has none at all. Rasmussen also suggested that *Mahgarita* had a lateral transverse septum resembling that of *Aegyptopithecus*, that there was an ectotympanic band fused to the petrosal, and probably not enough space for a free ectotympanic ring. However, restudy of these structures led others to refute these suggestions and reaffirm that *Mahgarita* was adapid-like in tympanic position and morphology (Ross 1994).

Asiatic Sivaladapids and Primitive Adapiforms

The family Sivaladapidae is restricted to Asia, where the sivaladapines survived until the Late Miocene. The subfamily Hoanghoniinae is naturally placed near them. Here will also be placed the recently described Early Eocene Asiadapini, which are probably related to them, and other more divergent Asiatic adapiforms. This radiation is, on the whole, poorly documented: no skull has yet been described. The best-known members of the group were until recently the Miocene sivaladapines, for which upper and lower jaws allow a description of their dental adaptations. Very high-crested molars and highly molarized P4/4 indicate a folivorous adaptation. A similar adaptation seems to be present in the Late Eocene–Early Oligocene genus *Guangxilemur*. First described through *G. tongi*, known by one M2/ and one upper canine from the Gongkang Formation of Guangxi Province, China (Qi and Beard 1998), its analysis was completed by the description of the Early Oligocene *G. singsilai* from Pakistan (Marivaux et al. 2002). The M2/ of *G. tongi* has high crests, a mesostyle linked to the centrocrista contributing to W-shaped labial crests, and pre- and postprotocristae as divergent as in the Miocene sivaladapines. The main difference with the latter is its possession of large hypocone and pericone. *G. singsilai* differs by a smaller hypocone and pericone, and a straight centrocrista on M2/. It also shows a highly molarized P4/, a DP4/, a simple P/3 with very small and narrow talonid, and an M/1–2 with salient crests, broad paracristid not joining the metaconid summit, and big, close, and deeply separated entoconid and hypoconulid. This morphology relates *Guangxilemur* to *Hoanghonius stehlini* and its close relative *Rencunius zhoui*, both from Late Eocene beds of the Heti Formation, Shanxi Province, China (Gingerich et al. 1994). Both species bear the hallmarks of this group: lower molars with twinned entoconid and hypoconulid, and upper molars with a continuous lingual cingulum bearing hypocone and pericone and a wide trigon basin limited by very divergent protocristae. On the mandible of *Hoanghonius*, which bears M/2 and M/3, a continuous paracristid joins the metaconid anteriorly. On the mandible of *Rencunius*, which bears M/1–2 and P/4, the molars are more bunodont, M/1 bears a well-formed paraconid, and P/4 is simple with a small metaconid, very short rounded talonid shelf, and continuous cingulids. The M1/ of *Rencunius* resembles the isolated upper molar of *Hoanghonius* but differs in some details, such as a more lingually bulging pericone, larger conules, and less waisting of the posterior border. The associated P4/ of *Rencunius* is very simple, with a large paracone, smaller protocone, and well-formed preprotocrista. Another sivaladapid very close to the above-mentioned genera is *Wailaikia*, from the Late Eocene Krabi mine of Thailand. *W. orientale* is represented by a mandible bearing M/2 and M/3 (Ducrocq et al. 1995). Alveoli for the anterior teeth show that it possessed a long premolar series with an unreduced two-rooted P/2 and a relatively large canine. The continuous and transversely long paracristid and the twinned entoconid and hypoconulid leave no doubt that this species is a sivaladapid close to *Hoanghonius*. It differs from the latter by its broader lower molars and much shorter M/3 with a barely salient third lobe. The dentary is low and elongated, and it preserves a high coronoid process and the articular condyle.

The bizarre maxilla known under the name of *Lushius quinlinensis*, from the late Middle Eocene of Shanxi, might pertain to the same group. Considered an adapiform *incertae sedis* by Szalay and Delson (1979), its M2/ bears similarities with that of *Hoanghonius*, both in outline – the posterior half being narrower than the anterior one – and in trajectory of postprotocrista. It is more primitive with respect to its incomplete lingual cingulum, and more derived with respect to its extremely high paracone, metacone, and crests joining them. These constitute a high ectoloph recalling some ungulates and a very unusual morphology for primates. However, this specialization goes in a direction analogous to many high-crested sivaladapids, and thus its least unlikely affinities are probably with sivaladapids.

The Early Eocene beds of the Vastan Mine, Cambay Formation, Gujarat, India, are dated around 53 Ma. They have been yielding new adapiforms in the last years. *Marcgodinotius indicus* was named by Bajpai et al. (2005), *Asiadapis cambayensis* by Rose et al. (2007), and a synthesis on these taxa is provided by Rose et al. (2009). Both are small and primitive adapiforms, with global phenetic similarity with early European cercamoniines, but they also have interesting differences. The dentaries of *M. indicus* are elongated and slender and show a large canine, small P/1, two-rooted P/2, and some compression of the premolar series leading to an anterolingual shift of their root pairs. P/3–4 are simple; P/3 is higher than P/4, and the latter bears a small, low, little-differentiated metaconid. The lower molars have simple talonid basins. M/1 has a large paraconid in anterior (not lingual) position. M/2 has a shelf-like paracristid, and M/3 has a short trigonid with narrow and rounded paracristid, and also a very small and narrow third lobe. M1/ is remarkable for its overall triangular outline, with a lingual part much narrower anteroposteriorly than its labial part. It also has a strong parastyle, a posterolabially directed postmetacrista, a well-expressed posterior cingulum making a small hypocone shelf without cusp, and a very marked waisting of its posterior border. These characters differ markedly from those of *Donrussellia*, and several of them might be primitive, which would lead to a reappraisal of the adapiform ancestral morphotype. It would be important to find some M2/. *Asiadapis cambayensis* is larger than *M. indicus*. It differs from it by a single-rooted P/2, several details of the lower teeth (small paraconid present on some M/2–3, larger third lobe on M/3), and the upper teeth showing more massive outlines and proportions as well as a well-formed crista obliqua almost continuous to the tip of the metacone. Some characters of this species are again quite different from those of cercamoniines; for example, some M/2–3 have a deep groove between protoconid and metaconid, and an M1/ has a preprotocrista leading to a paraconule and continuing toward the tip of the paracone. The differences noted between these two genera and European cercamoniines underline a marked systematic separation between the two groups.

Several limb bones of these asiadapines have been described (Rose et al. 2009). A beautiful complete humerus shows a rounded head, a prominent and low greater tubercle, a salient deltopectoral crest slightly overhanging the bicipital groove, and a proximally extended brachialis flange. Its distal extremity shows a spherical capitulum projecting distally beyond the trochlea, a well-formed intercondylar groove, a conical trochlea projecting only very slightly distally (more than in *Cantius* and *Notharctus*, less than in the omomyiforms *Microchoerus* and *Shoshonius*). Its characters are in overall agreement with a generalized arboreal quadruped. Proximal radii show a slightly ovoid head (slightly rounder than in *Cantius*, but less than in living galagos). Two femora have a subspherical head and a long neck making an angle relative to the shaft near 57°, as in adapoids and living lemurs. The greater trochanter does not project as far proximally as the head. The trochanteric fossa is deep, narrow, and bordered by a salient paratrochanteric crest. A small third trochanter is distal, opposite to the distal part of the lesser trochanter. The femoral shaft is elongate and comparable to that of *Cantius*, *Notharctus*, and living lemurs. However, the distal extremity is not as high anteroposteriorly as in these fossils or in leaping prosimians. Again, the femora fit with the notion of an active arboreal quadruped. Tarsals have also been found, 11 calcanea and 5 astragali. These fall into two size classes and probably pertain to more than two species. The three larger partial calcanea, probably belonging to *A. cambayensis*, appear very similar to, but smaller than, those of *Cantius*. Among the smaller ones, four appear again similar (probably *M. indicus*) and four differ slightly in proportions, having a shorter proximal and a longer distal part, indicative of increased leaping propensities. It is difficult to establish whether these differences reflect a different species or merely extensive intraspecific variability (Rose et al. 2009). One large and four smaller astragali are very similar to those of notharctids. Only one of them has a lower neck angle, closer to those of omomyids and eosimiids. However, relative neck length is more discriminant of primate groups, and by that measure these astragali are like those of notharctids. The postcranials as a whole reflect the adaptations of small active arboreal quadrupeds. In conjunction with tooth dimensions, the postcranials permit relatively good weight estimates for these species, which are around 100–120 g for *M. indicus* and 250–300 g for *A. cambayensis* (Rose et al. 2009).

Asiatic adapiforms of late Early and early Middle Eocene age are restricted to small species from Pakistan. The Early Eocene Gandhara Quarry yielded an assemblage of *Panobius russelli*, which shows interesting characters (Gunnell et al. 2008). M/2 in the holotype dentary is remarkably primitive due to its large lingual paraconid, well separated from the metaconid, and a P/4 that is more elongated and posteriorly narrower than in *Donrussellia*. The sole illustrated M1or 2/ is very transversely elongated, due to the extended lingual slope of the protocone. *Panobius* might have some dental characters more primitive than in *Marcgodinotius*, and it probably would add to a reconstruction of the primitive adapiform morphotype. Two other species, *P. afridi* and *P. amplior*, are from the younger locality of Chorlakki, early Middle Eocene, and are more fragmentarily known (Russell and Gingerich 1987; Gunnell et al. 2008). *Sulaimania arifi* from the Gandhera Quarry is known only through an isolated M/2, revealing a small adapiform with a continuous anterior paralophid, reminiscent of some anchomomyini.

Four genera of small Asiatic adapiforms have been described from Late Eocene and Early Oligocene beds of Thailand, Burma, and Pakistan. They are all known by very fragmentary material. The first described, *Bugtilemur mathesoni* from the Early Oligocene of Pakistan, is also the best known, being represented by some upper teeth in addition to lowers (Marivaux et al. 2001). Its upper molars are simple, with a continuous lingual cingulum, no hypocone and conules, a postprotocrista posteriorly directed, and a posteriorly opened trigon basin. A high centrocrista is reported as shared-derived with living *Cheirogaleus*. The lower molars have a short trigonid with metaconid posterior to the protoconid, a broad talonid basin rounded posteriorly, and an anteriorly directed cristid obliqua. The P/4 is elongated, molarized with a narrow trigonid and a broad talonid basin with a small entoconid. Many dental similarities with *Cheirogaleus* led a parsimony analysis to place *Bugtilemur* as a sister group of *Cheirogaleus*, nested within the Malagasy lemuriform radiation, despite its lower canine not having the morphology of a tooth comb canine. The subsequent description of a small mandible from the Late Eocene of Thailand, named *Muangthanhinius siami*, revealed important features: an elongated and low dentary, a two-rooted, high and unreduced P/2, a partial canine root that is large and relatively vertically implanted – all suggestive of adapiform affinities. Some differences notwithstanding, P/3 to M/1 show a remarkable general similarity with those of *Bugtilemur* (Marivaux et al. 2006), which established adapiform status for both genera.

Four isolated teeth from two different localities of the Pondaung Formation, late Middle Eocene of Myanmar, were described as the smallest sivaladapid species, *Paukkaungia parva* (Beard et al. 2007). The M/1 is primitive by its broad trigonid with large paraconid and extended trigonid basin. Its talonid is broad and rounded in outline. It is possible to identify a hypoconulid and an entoconid among the poorly differentiated posterolingual cusps, making this species reminiscent of other sivaladapids. The P/3 and P/4 attributed to this species have a protoconid which is very extended anteroposteriorly and at the same time low. They have a sloping talonid basin restricted lingually by the posterior extension of the postprotocristid. P/3 has a low crestiform hypoconid, P/4 had a better differentiated one (worn) and a small entoconid. The roots of P/3–4 show a partial coalescence, suggesting a trend toward premolar compaction (Beard et al. 2007). Their unusually low relief might have been linked to some anteroposterior overlapping. They are intriguing in any event. The other species, *Kyitchaungia takaii*, is based on one isolated M/2 that is partially eroded. It is larger than *Paukkaungia parva*, and its entoconid and hypoconulid are better differentiated. Some postcranials are referred to this species. A calcaneum is relatively similar to those of the notharctids, although it differs from them by a broader proximal facet and a deep medially offset cuboid pivot. The curvature of its proximal part is marked. An astragalus without head also resembles those of small notharctids. A proximal femur from the same locality, attributed to the same individual as the tarsals, has been described in detail (Marivaux et al. 2008). It reflects good hip mobility. All of these elements in *Kyitchaungia* suggest a broad locomotor repertoire with quadrupedalism, including some leaping, climbing, and possible suspensory activities.

On the whole, the Asiatic adapiforms remain poorly known, with no skull described, many taxa known only by fragmentary dental remains, and a recently expanded but still limited postcranial record. Various recent discoveries have substantially increased our knowledge, confirming that the Asiatic adapiform radiation probably played a central role as the source of dispersals into Europe, North America, and Africa. However, much more remains to be discovered.

Eocene Lemuriformes, Stem Lemuriforms, and the Concept of Strepsirhini

Eocene Lemuriformes

Living lemuriforms can be easily distinguished from fossil adapiforms by the possession of a dental complex, the tooth comb, formed at the anterior extremity of the lower jaws by the closely appressed and proclive lower incisors and canines. Recurrent speculations about the affinity of some adapiform genera, lately anchomomyins, with the Lemuriformes were put to rest by the discovery in Africa of Eocene lemuriforms bearing a tooth comb (Seiffert et al. 2003). Found in the Egyptian Fayum stratigraphic sequence, they come from the two localities seen above for the two adapids. *Saharagalago* and *Karanisia* come from BQ–2, early Late Eocene (around 37 Ma), and *Wadilemur* from L-41, a Latest Eocene locality (Seiffert et al. 2005a; Seiffert 2006). They are all small primates whose upper molars have a well-formed cingular hypocone, protocone crests surrounding an anteroposteriorly broad trigon basin, and a sharply defined postprotocrista joining the metacone on *Karanisia* and *Saharagalago*, but not reaching its summit in *Wadilemur*. The lower molars have an anteroposteriorly compressed trigonid without paraconid and with a long paracristid often joining the metaconid summit. *Karanisia* is peculiar by its continuous lingual cingulum and extensive hypocone shelf, with small crestiform hypocone. Its P4/ and P3/ have a broad protocone lobe and cusp, with P4/ also showing a continuous lingual cingulum. A lower dentary of *W. elegans* shows procumbent incisor and canine alveoli, and P/2–4. P/2 and P/3 have crowns which project anteriorly with some overlap of successive teeth. P/4 has a well-formed talonid basin, with a tall labial hypoconid and a long acute cristid obliqua. This morphology is reminiscent of later galagids. A partial femur ascribed to *Wadilemur* presents characters reminiscent of those of living galagids, e.g., a cylindrical femoral head, suggesting frequent leaping in its repertoire, but less specialized than in the vertical clinging and leaping galagos. *Wadilemur* and *Saharagalago* are interpreted as stem Galagidae, and *Karanisia* as a stem lorisoid (Seiffert et al. 2003, 2005a). This implies that the split between lorisoids and the Malagasy lemuroids would be older than Late Eocene; however, the lemuroid morphotype is unknown. Two genera found in the Early Oligocene of Oman, *Omanodon* and *Shizarodon*, are known only by isolated teeth and have remained relatively enigmatic (Gheerbrant et al. 1993). Dental similarities between *O. minor* and *S. misrensis* suggest that they probably belong to the same group of early lemuriforms (Godinot 2006).

Stem Lemuriformes

Two distinct genera can be placed in a family named the Djebelemuridae, which are now assumed to be stem lemuriforms – which means, closely related to Lemuriformes but not possessing their defining apomorphy, the tooth comb. *Djebelemur martinezi* occurs in the late Early or early Middle Eocene locality of Chambi, Tunisia (Hartenberger and Marandat 1992; Marivaux et al. 2013). The type mandible preserves P/3–M/3, and alveoli for a moderate-sized canine and P/2. P/3 and P/4 are very simple, elongated and narrow, relatively low, bearing a continuous lingual cingulid and a simple talonid cusp. The lower molars have long paracristids joining the metaconid summit. An isolated lower canine and P/2, and a maxilla bearing P3–M3/, were added recently. P/2 is single-rooted, moderate in size, slightly procumbent. The canine is surprisingly small, and also somewhat procumbent. The upper molars have a trigon resembling that of Eocene lemuriforms, but there is no hypocone, whereas there is an almost complete lingual cingulum, interrupted only lingually to the protocone summit. P3/ and P4/ are triangular in outline, P4/ having a small and low protocone, and P3/ only a cingular cuspule. The polarity of these premolar characters is intriguing: primitive or secondarily simplified? An astragalus from Chambi shows the typical characters of small strepsirhines, with a strongly sloping fibular facet and a posterior trochlear shelf with a laterally offset groove for the flexor fibularis tendon. The elongated neck and tightly curved profile of the trochlea suggest that leaping was a part of its locomotor repertoire (Marivaux et al. 2013). Isolated petrosals from Chambi also pertain to *Djebelemur* or to a small azibiid present in the fauna. Their detailed study with micro-CT-scan reveals interesting characters (Benoit et al. 2013). Among them are a stapedial and a promontory artery that are very small and suggest that the internal carotid was supplemented by another vessel.

Another more recent species, awaiting a new generic name, is *“Anchomomys” milleri* from the L-41 locality, Latest Eocene of the Fayum, Egypt (Simons 1997). A mandible bearing all teeth from canine to M/2 shows M/1–2 similar to those of *Djebelemur*, and broader P/3 and P/4, the latter having a second crest descending posteriorly from the protoconid summit (Fig. 11). P/2 is somewhat smaller than P/3, not reduced. The canine is larger than P/4, low with a curved anterior border and a relatively low and rounded summit. Its crown is slightly procumbent, but the root is rather vertical. Its continuous lingual cingulid becomes posteriorly higher above the crown base, all this giving it a premolariform appearance. Both *Djebelemur* and *“A.” milleri* clearly did not possess a tooth comb, yet their canines are no longer the high pointed canines of primitive adapiforms; they are low and slightly procumbent, probably illustrating a step in the transformation of a primitive canine into a procumbent tooth comb canine. Phylogenetic analyses recover the place of djebelemurids as stem lemuriforms, along with *Plesiopithecus* (Seiffert et al. 2005; Marivaux et al. 2013).

Plesiopithecus teras is a very unusual primate found in Quarry L-41 of the Fayum. Its lower mandible bears an enormous, procumbent anterior tooth which is a lower incisor or a canine, followed by a very reduced canine or P/1. The lower premolars are simple; they are broader, lower, and more anteroposteriorly compressed than in djebelemurids. The lower molars likewise have anteroposteriorly

Fig. 11 Lower teeth of the stem lemuriform *“Anchomomys” milleri* from the Fayum in occlusal (**a**) and lingual (**b**) views. The anterior tooth on the *left* is a canine, which is relatively low and premolariform. It is followed by long and narrow P/2 and P/3, a larger P/4, and two molars, which have a short trigonid without a paraconid. SEM of casts

compressed trigonids with long paracristids, and they also are much broader and lower than in djebelemurids. There is sometimes a metastylid, and M/3 is much shorter than in *Djebelemur*, having a very abbreviated third lobe. A distorted cranium shows upper molars decreasing in size from M1/ to M3/ (Simons and Rasmussen 1994). They are relatively simple, with a continuous lingual cingulum but without hypocones. Whereas P4/ is transversely broad, P3/ is single-cusped and the small P2/ is bilaterally compressed. There is a very large vertical canine, inserted in a high muzzle. The roof of the cranium is anteroposteriorly arched. The orbits were large and indicate nocturnal habits. *Plesiopithecus* is highly autapomorphic. Its lower jugal teeth recall djebelemurids and lorisoids, and the very large lower tooth could indicate an enlarged tooth comb canine accompanied by incisor loss (Simons and Rasmussen 1994). This scenario or possible ties with *Daubentonia* (Godinot 2006) would imply a lemuriform status, whereas scenarios from a more primitive djebelemurid state imply a stem lemuriform status as found in the cladistic analyses.

Azibiidae

It took recent recovery of sufficient dental remains for researchers to better realize what these bizarre primates probably are. They occur in late Early or early Middle

Eocene localities of North Africa. After the initial description of *Azibius trerki* from the Gour Lazib, Algeria, by Sudre (1975) as a probable prosimian, the dentary of this genus was later disputed. Its high and roughly blade-like P/4 was so unusual that the primate status of the genus was doubted (Szalay and Delson 1979). Isolated molars of the smaller *Algeripithecus minutus*, found in the close Glib Zegdou, Algeria, are extremely bunodont, and its M2/ is so similar to that of some parapithecids that its anthropoid status received general agreement (Godinot and Mahboubi 1992, 1994). However, more complete material recovered later revealed that the two genera were close to each other and led researchers to synonymize two other genera (Tabuce et al. 2009). A dentary of *Algeripithecus* shows a tooth row increasing in height from a low M/3 to an M/1 with elongated and high trigonid, to long, high and blade-like P/3–4, P/4 with two successive summits, P/3 with a second summit, presumably a metaconid, smaller and lower than the protoconid. P/3 and P/4 have complete labial and lingual cingulids showing an anterior elevation. Anterior alveoli are interpreted as those of a small single-rooted and procumbent P/2 and of a large canine, procumbent and with a long posterior root lingual to the roots of P/3. The upper teeth are all isolated. The upper molars are extremely bunodont. The transversely elongated M2/ has a large hypocone, almost as high as the protocone, a metaconule, and an extended labial slope of the paracone. The anteroposterior crests on the paracone and metacone are salient. M1/ is less transversely broad, and its paracone is higher, with steeper slopes. P4/ has two labial cusps, the larger one being a high peak, in profile view, with a high labial slope suggesting some exodaenodonty (enamel extended beyond the alveolar margin, along the roots). The tooth is transversely short, with the lingual lobe bearing two small cusps, a small pointed protocone and a smaller hypocone. The high P3/ seems to have one large cusp. A smaller transversely compressed P2/ is associated with the others.

The dentition of *Azibius trerki* is roughly similar but also shows some differences. Aside from its larger size, it is even more bunodont, and its P3–4/ are more transversely extended and more molarized: P4/ has a recognizable trigon basin and paraconule, and P3/ a small protocone lobe. A small portion of maxilla bearing P3/ and P4/ revealed a large infraorbital foramen, the trace of a lacrimal canal oblique anteroventrally, and a part of the orbital floor suggesting that the orbits were large, as in nocturnal primates. All these characters are more typical of strepsirhines (or omomyiforms), and the phylogenetic analysis of Tabuce et al. (2009) placed azibiids as primitive sister group of a clade (dejbelemurids + lemuriforms). In the future, such a position as stem lemuriforms might even be shifted within lemuriforms, if the long procumbent lower canine of *Algeripithecus* turns out to be as reminiscent of a tooth comb canine as the authors suggest. Strepsirhine affinity is confirmed by the description of an astragalus ascribed to *Azibius* and a larger to a larger undescribed species of the same group. These astragali show the laterally sloping fibular facet typical of strepsirhines (Marivaux et al. 2011). Researchers have inferred quadrupedal and climbing abilities for this species that are similar to those of living cheirogaleids. One of the most intriguing aspects of these azibiids has received little attention until now, namely the adaptive significance of their dental specialization. Most living and fossil lemuriforms of small size are highly insectivorous. What may have been the diet of *Algeripithecus*, whose body weight is estimated between 65 and 85 g?

The Concept of Strepsirhini

A number of shared derived characters, which will be detailed below, unite tarsiids and simians in a monophyletic clade, the Haplorhini. By contrast, living Lemuriformes and Strepsirhini appear basically primitive. This is not a problem for living lemuriforms, which can easily be diagnosed by their possession of the tooth comb, a derived character. However, it becomes critical when one considers the place of fossil adapiforms, which are most often considered strepsirhines. Such an affinity has long been assumed, based on their possession of middle ear characters extremely similar to those of living lemurs. The bulla, the free tympanic ring inside of it (formed by the ectotympanic), the carotid entry into the bulla, and the arterial circulation inside it are extremely similar in adapid and living lemur crania (Stehlin 1912). However, inasmuch as these characters have long been considered primitive in primates, they do not prove close affinity. Nevertheless, detailed morphological and embryological studies enable us to identify possible synapomorphies. The truly annular ectotympanic is a specialized retention of a fetal character limited to adapiforms and lemuriforms, and rarely found elsewhere among mammals (among which most "ring-like" ectotympanics are in fact slightly expanded; MacPhee 1981, 1987; MacPhee and Cartmill 1986). Another potential synapomorphy is a gap existing in the annular bridge connecting the ectotympanic and the bulla wall ("recessus dehiscence"; Beard and MacPhee 1994). Furthermore, clearly shared-derived between adapiforms and lemuriforms are a suite of characters issued from studies of postcranial anatomy. Several characters of the astragalus – a laterally sloping fibular facet, a position of the groove for the flexor fibularis tendon offset from the posterior trochlear facet, a long posterior trochlear shelf – are derived and found in both adapiforms and lemuriforms. They are complemented by characters of the distal tibia and the navicular (Dagosto 1985; Gebo 1988; Covert 1988). This suite of characters indicates increased hallucial opposability, more habitually inverted foot postures, and foot flexion/extension accompanied by some conjunct rotation at the upper ankle joint. So far, there is no evidence of convergent acquisition of these characters, some of which are found in stem lemuriforms (Marivaux et al. 2011, 2013). These characters are probably strengthened by hand characters: adapiform hands have a structurally divergent thumb, as do those of lemuriforms, probably derived relative to simian hands (Godinot 1992b). However, this depends on the reconstruction of the primitive primate morphotype, which is under debate (see below in anthropoid origins part). Early omomyiform and simiiform hands are almost unknown. In any case, regardless of possible hand characters, strepsirhine monophyly appears well established.

The Omomyiformes Radiations

Besides adapiformes, many smaller fossils have been described in Eocene times; these are either united in one family, the Omomyidae, or spread out over two – the Omomyidae for the North American forms and Microchoeridae for the European ones. For a long time, these small forms were found to be "tarsier-like" and referred to an infra-order Tarsiiformes. They have also been suspected to possibly include anthropoid ancestors. However, the so-called similarities with *Tarsius* were exaggerated. Most omomyids have large eyes due to their small size and nocturnal adaptation; yet these eyes are no larger than in living small nocturnal strepsirhines. Despite new discoveries, recurrent re-analyses of fossils, and increasingly sophisticated phylogenetic analyses, it has proven impossible until now to identify among the Omomyidae a group which would be a consensual sister group of Tarsiidae. Moreover, most of these fossils appear not to possess the characters indicating anatomical haplorhinism (explained below for Tarsiidae). Thus, for the sake of clarity and consistency, these omomyids should not be included in Tarsiiformes. A number of omomyid groups had their own history and became extinct without showing any trace of evolution toward tarsiid or simian characters. The best choice is to place them in the taxon Omomyiformes, proposed by Schmid (1982), which has been adopted by a growing number of specialists (e.g., Ross et al. 1998; Williams et al. 2010). That is probably a paraphyletic grouping, but it is not appropriate to transfer some of them to a useful Tarsiiformes until it can definitively be shown that the group is a sister group to tarsiids. This is an ongoing debate, to which we will return below after discussion of the Tarsiidae. There are more than a hundred species of omomyiforms, found on three continents, which indicates a complex history for this broad group.

The Stem Genus *Teilhardina*

The genus *Teilhardina* is exceptional in many respects. Found on three different continents in the Earliest Eocene, it appears at the base of the later diversification of several subfamilies. As such it is paraphyletic and represents one of the goals of paleontologists: to identify an ancestral genus, a true stem genus at the base of the evolutionary diversification of entire families or subfamilies. This genus was first described from dental remains from the Belgian locality of Dormaal, and was named "*Omomys*" *belgicus* (Teilhard de Chardin 1927). The species was removed from *Omomys* and placed in a new genus *Teilhardina*, as *T. belgica*, by Simpson (1940). The same genus was later identified in an Early Eocene locality from the Willwood Formation, Wyoming, by Bown (1976), who named it *T. americana*. Several other North American species were subsequently named (see below). Eventually, the genus was also discovered in China. A cranium and associated mandibles, named *T. asiatica*, increased our knowledge of the genus substantially (Ni et al. 2004). One species has also been named from

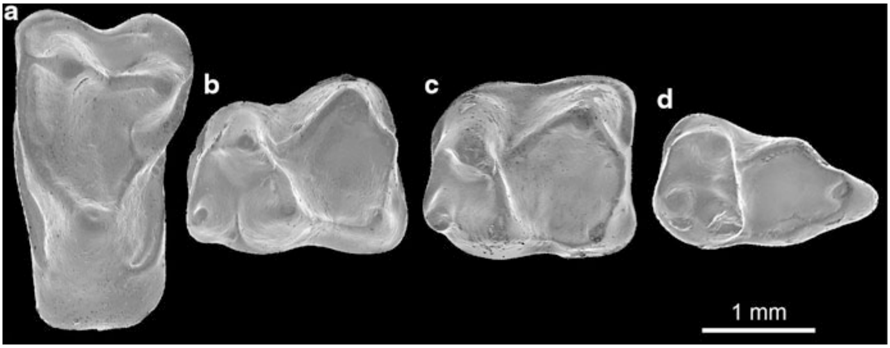

Fig. 12 Isolated teeth of *Teilhardina belgica* from Dormaal, Begium, all in occlusal view. The M2/ (**a**) is very simple and primitive, transversely elongated without hypocone or protocone fold; however, there is a slight lingual thickening of the posterior cingulum. Lower molars are M/1 (**b**), M/2 (**c**), and M/3 (**d**); M/1 and M/3 appear primitive through their large trigonid with a large paraconid. SEM of casts

the Tuscahoma Formation of Mississippi (*T. magnoliana*, Beard 2008). Linked to the rapid warming of Paleocene–Eocene boundary events, *Teilhardina* spread from Asia to the two other continents – probably through Europe to North America (*T. belgica* and Earliest Eocene American *T. brandti*, Smith et al. 2006). Species of *Teilhardina* are very small, with dentally estimated body weights around 30 g, similar to the smallest living primates. They have a very primitive dentition, with four premolars, a tiny metaconid on P/4, lower molars with a large paraconid on M/1, reducing on M/2 and M/3, and upper molars without hypocone (Fig. 12). The cranium is the oldest known for primates. It shows a broad and rounded braincase and probably featured a somewhat shortened snout. Its orbits are smaller than in any other omomyid, probably reflecting diurnal habits. In contrast, most later omomyiforms are considered to have been nocturnal. These orbits are convergent (angle estimated at 51°) and the interorbital breadth is narrow (Ni et al. 2004). The infraorbital foramen is relatively large. In the case of *T. belgica*, postranials are known (Szalay 1976). A moderate elongation of its calcaneum suggests leaping abilities and a locomotor repertoire close to that of living cheirogaleids.

North American Anaptomorphinae

Among the North American Omomyidae two subfamilies are recognized, succeeding each other in abundance through time: species of Anaptomorphinae are the most abundant during the Early Eocene, whereas Omomyinae become dominant during the Middle Eocene. Several clades of anaptomorphines can be recognized in the Early Eocene (Bown and Rose 1987). Some of the Middle Eocene followers can be linked to these clades whereas others are more difficult to root in the earlier forms.

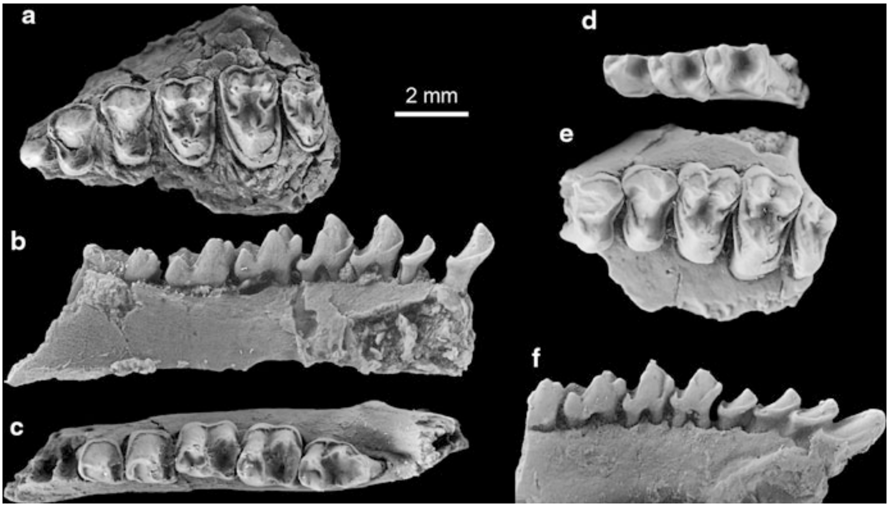

Fig. 13 Dentitions of primitive North American anaptomorphines, *Teilhardina* and *Anemorhysis*. Maxillae of *Teilhardina* intermediate between *T. americana* and *T. crasssidens* in occlusal view (**a**) and of *T. crassidens* (**e**); mandibles of *T. americana* in lingual view (**b**), *T. crassidens* in occlusal view (**c**), and intermediate between the two species in lingual view (**f**). Left mandible of *Anemorhysis sublettensis* in occlusal view (**d**). The anterior incisor is enlarged in the lineage (**f**), and the canine in the intermediate specimens (**f**) is more reduced than in *Teilhardina americana* (**b**: from right to left canine, small P/2, P/3, P/4, M/1-2-3). Photographs of white-coated epoxy casts, all at the same scale

The first clade, that of *Teilhardina-Anemorhysis*, starts from *T. americana*. In the exceptional fossil record of the Bighorn Basin, Wyoming, a series of assemblages links the species *T. americana* and *T. crassidens* through intermediate assemblages (Bown and Rose 1987). The whole lineage has an I/1 relatively enlarged in comparison with *T. belgica* or *T. brandti* (Fig. 13). This anagenetic lineage shows a slight diminution in size, broadening of the cheek teeth, lowering of P/3 and P/4 which become more molarized (P/4 with larger paraconid and metaconid, P/3 with small metaconid), a small mesostyle present on M1/, variable on M2/. A very rare smaller species *T. tenuicula* occurs later. In the Bighorn Basin, species of *Anemorhysis* show up later as punctuated occurrences, showing that the lineage was evolving elsewhere and species were entering from time to time in the Basin. The five species of *Anemorhysis* have a wide geographic distribution in the Early Eocene of Wyoming, Utah, and North Dakota, surviving in the earliest Middle Eocene of Wyoming. They differ from *Teilhardina* and *Tetonius* species by their more molarized P/4, lower molars with sharp cusps less basally inflated than in *Tetonius*, anteriorly broad talonid basin and straight postcristid (Fig. 13). P/4 has a well-developed metaconid, a prominent paraconid, and a well-developed talonid basin with hypoconid and small entoconid. *A. savagei*, from the Washakie and Wind River Basins (Lysite, Wa6), Wyoming, is considered a structural intermediate between *Teilhardina* and later *Anemorhysis* species (Williams and Covert 1994).

It is small, retains a P/2 and has relatively simple P/4. *A. wortmani* and *A. sublettensis* have P/4 with a large paraconid close to the metaconid, and the second is further derived by its long and broad talonid basin. *A. pattersoni* is larger and has a low and weak P/4 paraconid. *A. natronensis*, from the earliest Bridger, is distinct through narrow lower molars, a very large entoconid on P/4, and I/1 only slightly larger than I/2.

It is possible that this clade gave rise to *Arapahovius*. The difficulty of making systematic decisions involving morphologically close species, even ones represented by abundant dental material, is illustrated by *Tetonoides pearcei*. Since its creation by Gazin (1962) this species has many times been placed in *Anemorhysis*, then subsequently removed and placed again in a valid genus *Tetonoides*. Lately, Gunnell and Rose (2002) listed it as an *Anemorhysis* species. Cuozzo (2002) showed that Late Graybullian material assigned to *T. pearcei* differs only in very subtle details from Lysitean specimens referred to *A. savagei*, implying that both be placed in *Anemorhysis*. However, Tornow (2008) determined *T. pearcei* to be in the position of a separate genus related to *Arapahovius*, and listed a second species, *T. coverti*, that was named in a dissertation. The message is that these species are very close to each other. It is possible that artifacts of cladistics and nomenclature are blurring the incipient divergence of lineages.

Contrary to *Tetonoides, Arapahovius* differs by marked characters. Found in the upper part of the Wasatch Formation (Lysite equivalent), Wyoming, *A. gazini* is characterized by crenulated enamel on all molars and upper premolars (Savage and Waters 1978). The upper molars are transversely elongated, bear a well-formed protocone fold, conules with marked pre- and postcristae, and an incomplete lingual cingulum without hypocone. On the dentaries, alveoli show its I/1 to have been moderately enlarged, with I/2 and C being smaller. P/3 and P/4 are moderately molarized, and P/2 is reduced. M/2–3 have broad and anteroposteriorly short trigonids. Tarsals of *Arapahovius* include an astragalus which has an elongated neck, a tibial trochlea with lateral ridge higher than the medial one, a posterior trochlear shelf, and a very rounded head. Partial calcanea present a short anterior part and a distal elongation indicating leaping propensities. A navicular and a cuboid are both moderately elongated, contributing to foot elongation as in *Hemiacodon* (see below). A smaller and more primitive species, A. *advena*, has been found in the Bighorn Basin (Bown and Rose 1991).

A second clade that is well identified in the Early Eocene is represented by the *Tetonius-Pseudotetonius* group. At the beginning, it is still very close to some *Teilhardina*. It contains the remarkable series of assemblages linking *T. matthewi* to *P. ambiguus* through intermediate assemblages that have been difficult to name (Fig. 14). This series illustrates one of the most beautiful anagenetic lineages showing progressive morphological change through time, in the ideal context of regional stratigraphic superposition (Bown and Rose 1987). This lineage displays a progressive increase in size of I/1 and P/4, and reduction of the teeth which are between them. In *T. matthewi*, I/1 is large and P/3–4 have a normal size relative to M/1. At the end of the lineage, I/1 has become enormous, P/4 is strongly enlarged relative to M/1, one tooth has been lost, and the others are crowded and reduced,

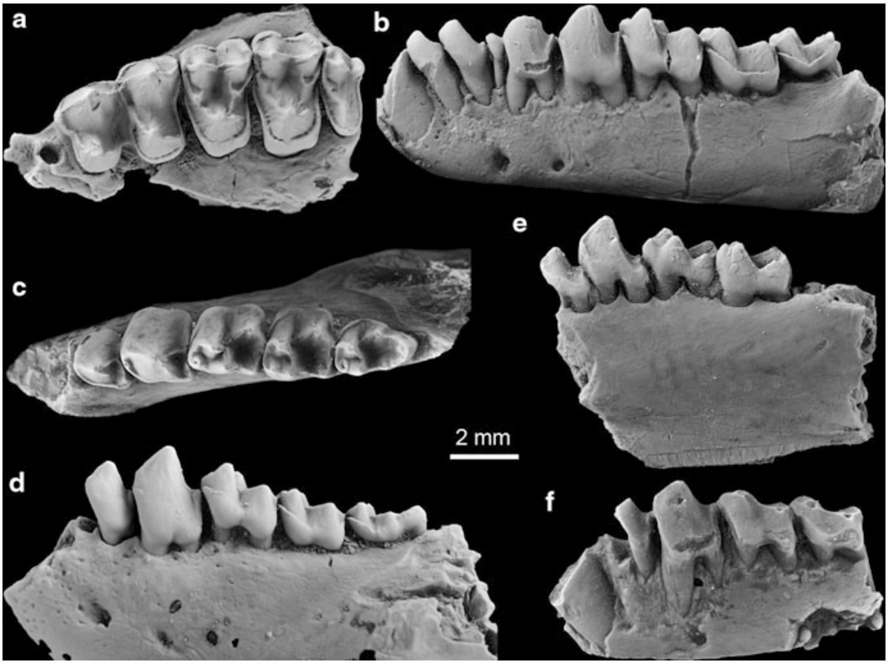

Fig. 14 The lineage *Tetonius-Pseudotetonius*. Maxilla (**a**) and mandible (**b**) of *Tetonius*; mandible of an intermediate, stage 3 of Bown and Rose (1987), in occlusal (**c**) and lingual (**d**) views (**d** inverted for comparison); two mandibles of *Pseudotetonius* in lingual (**e**) and labial (**f**) views. There is a marked difference between the mandible of *Tetonius*, with a large P/3 and three teeth between P/4 and the large incisor (**b**), and that of *Pseudotetonius*, with a very small P/3 and alveoli for two other small teeth between the large anterior incisor and P/4 (**f**). The intermediate stage (**c** and **d**) shows a moderately reduced P/3. Photographs of white-coated epoxy casts, all at the same scale

justifying a different generic name. Intermediate assemblages show some reduction of I/2 and C, the loss of P/2, and a progressive reduction of P/3, which becomes single-rooted and later very small. Changes occur not abruptly but through displacements in variations. The process of anterior incisor increase linked to a reduction of the teeth between it and P/4 or P/3 is a common evolutionary trend, usually explained by selection on anterior incisor function. The small *Tatmanius szalayi*, which has a high pointed P/4 without metaconid, is considered a likely descendant of *Pseudotetonius* (Bown and Rose 1991).

Tetonius is a well-known genus. The skull of *T. homunculus* is known since its description by Cope in 1884, and it has been restudied since (e.g., Szalay 1976). The cranium is broad and short in dorsal view. A large orbit is circumscribed by a complete postorbital bar. The cranium is incomplete and crushed. A remnant of bulla wall shows that the bulla was large. In its accessible details, such as the promontory canal included in a septum, Szalay (1976) found it very similar to *Necrolemur*. The dental formula was discussed by earlier authors. Szalay (1976)

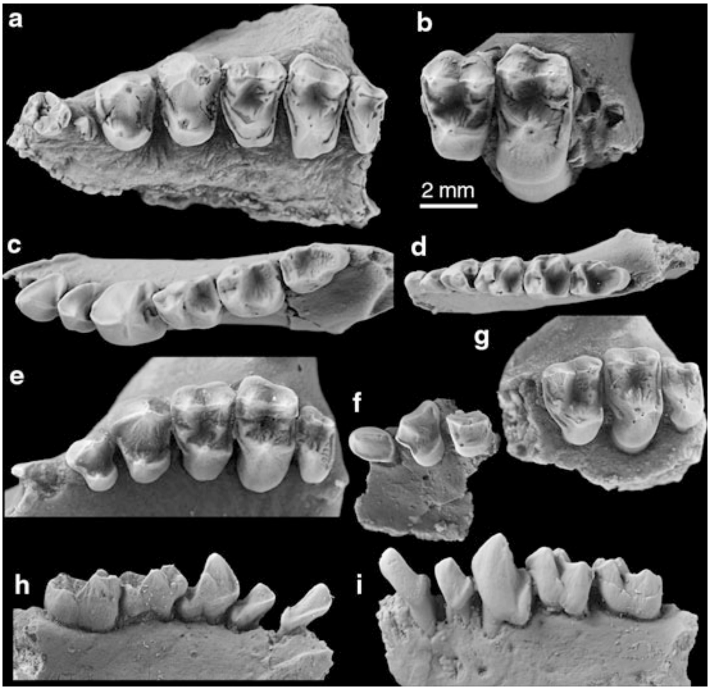

Fig. 15 *Absarokius*, other derived anaptomorphines, and *Trogolemur*. Maxilla of *Absarokius abbotti* (**a**) and mandible of *A. nocerai* (**c**). Maxilla of *Gazinius amplus* (**b**), mandible of *Trogolemur myodes* (**d**), and maxilla of *Strigorhysis bridgerensis* (**e**). Upper dentition (**f** and **g**) and mandible (**h** and **i**) of *Aycrossia lovei*. (**f**) shows P2/, P3/, and the lingual part of P4/. All are occlusal views, except for (**h**), which is lingual, and (**i**), which is labial. Photographs of white-coated epoxy casts, all at the same scale

identified isolated teeth and reconstructed *T. homunculus* as having enlarged anterior incisors, smaller roughly similar-sized I2 and canine, and very reduced P2 above and below. The P4 are slightly enlarged above and below, the lower one being higher than the molars and P/3. P/3 and P/4 are simple, P/4 being broad with reduced or absent metaconid and paraconid. M2/ is transversely elongated. M1/ and M2/ have a protocone fold, small conules, and a complete lingual cingulum (Fig. 14). The lower molars have a lingually placed paraconid that is large on M/1, smaller and closer to the metaconid on M/2–3. The M3s are reduced.

The third clade of anaptomorphines which is differentiated in the Early Eocene is that represented by species of *Absarokius*, its close derivatives *Strigorhysis* and *Artimonius*, and Middle Eocene genera considered to be descendants of this group, namely *Aycrossia* and *Gazinius* (Fig. 15), as well as possibly *Anaptomorphus*. The genus *Absarokius* is characterized by enlarged upper and lower P4, associated with incisors much smaller and M3 more reduced than in *Tetonius*. In the rich and detailed record of the Bighorn Basin, Bown and Rose (1987) distinguish two divergent specific lineages, *A. metoecus* and *A. abbotti*, both showing anagenetic change through time and giving rise to two different genera. The lineage of *A. metoecus* shows trends toward transverse narrowing and trigon basin broadening on M/1–2, some ridulation of upper molar enamel, and labiolingual narrowing of the M/1 trigonid. These characters are found in the Late Wastachian, briefly occurring *A. gazini*, which has narrow lower molars and somewhat enlarged incisors. The *A. metoecus* specific lineage is giving rise directly to species of *Strigorhysis*, which split in the Early Bridgerian into *S. bridgerensis* and *S. huerfanensis*. There are three species of *Strigorhysis*, which differ from those of *Absarokius* by rugose enamel on all molars and upper molars in which the protocone fold has increased and joined the posterior cingulum to realize one strong posterior crest (postprotocingulum). These species are well represented in the Aycross Formation, Wyoming, and also the Willwood Formation of Wyoming and the Huerfano Formation of Colorado. The second lineage of *Absarokius, A. abbotti*, shows a tendency toward size increase, as seen in M/1–2 size, and increased hypertrophy and exodaenodonty of P/4 (ventral expansion of enamel on its labial side). These trends continue in the latest Wasatchian and earliest Bridgerian in three species formerly included in *Absarokius* and now included in the genus *Artimonius* (Muldoon and Gunnell 2002). In addition to the increase in P/4 hypertrophy, these species show different degrees of lower premolar crowding. They all have lost P/2. P/3 becomes single-rooted in *Artimonius nocerai* and *A. australis*, and P/3 is very reduced in *A. australis* and *A. witteri*. Several limb bones of *Absarokius* have been described (Covert and Hamrick 1993). A distal humerus shows the trochlea to be well separated from the capitulum by a groove. A distal tibia exhibits a proximally long facet for the fibula, reflecting close appression between the two bones. The omomyid-like astragalus shows a well-grooved trochlea, and the calaneum has an elongated anterior part (54 % of total length). These characters indicate a small quadrupedal and leaping primate (weight estimated around 200 g).

Aycrossia and *Gazinius* include three rare species, known by fragmentary material (Fig. 15). The first species were discovered in the Aycross Formation of Wyoming, which samples basin margin, upland areas (Bown 1979). *A. lovei* has a tall P/4, small two-rooted P/3, M/1 with large paraconid, transversely elongated M1–2/, M3 not much reduced. *Gazinius amplus* is a large anaptomorphine which has a transversely very elongated M2/ lacking conules, postparacrista, and protocone fold, and with a lingual part so expanded that the protocone is almost centrally placed. *G. bowni*, found in the Green River Basin, is represented only by one M2/, which is smaller than that of *G. amplus* and has a well-formed postprotocrista and protocone fold (Gunnell 1995a).

Chlororhysis and *Anaptomorphus* are also genera known by fragmentary material and difficult to relate closely to the other, better documented anaptomorphine lineages. *C. knightensis*, known by four specimens (Early Eocene), is similar to *Teilhardina* in retaining unreduced canine and P/2, but it has more crowded anterior teeth and P/3–4 with more developed lingual cingulid. Gunnell and Rose (2002) note that it is similar to the omomyine *Loveina*. *C. incomptus* differs by small details. Two or three species of *Anaptomorphus* are known later, during the Middle Eocene, separated from potential ancestral forms by a long gap. They remain very small species, generalized, which have lost P/2 and have small M3. The lower molars are slightly bunodont, with bulbous cusps. M2/ is transversely elongated with expanded lingual slope. M1–2/ have well-developed metaconules and protocone fold. *A. westi* differs in being larger; sometimes a third species, *A. wortmani*, is also distinguished by its smaller size (or it is lumped into *A. aemulus*). These species remain poorly known.

The genus *Trogolemur* is so distinctive that it has often been placed in a special tribe, the Trogolemurini. However, the content of the tribe is in debate. *Trogolemur* represents the extreme in the trend toward I/1 size increase common in anaptomorphines. Its lower incisor is so large that its root is posteriorly extended below the molars. *T. myodes* is known through a number of specimens from the Bridgerian (Br2 and Br3) of the Bridger Formation, southern Green River Basin, Wyoming (Gunnell 1995a), and from Nevada (Emry 1990) (Fig. 15). Slightly older species, *T. amplior* and *T. fragilis*, have been described from the earliest Bridgerian (Br1) of the Wind River Basin; however, these are very fragmentary (Beard et al. 1992). The genus *Sphacorhysis* has been erected for a species which shows a morphology plesiomorph in comparison with *Trogolemur* but is advanced in its direction in comparison with other genera. Several phylogenetic analyses have rooted *Trogolemur* (+*Sphacorhysis*) near *Anemorhysis*, postulating a sister group relationship of this clade with *Tetonoides* and *Arapahovius*. However, the content of such an extended tribe of Trogolemurini is not consensual among specialists (e.g., *Arapahovius* + *Tetonoides* are rooted in *Teilhardina crassidens* according to Tornow 2008).

Omomyinae

The subfamily Omomyinae is a beautiful example of mosaic evolution during a phase of diversification. Starting with the Early Eocene generalized genus *Steinius*, a rapid diversification leads to a large number of genera in the Middle Eocene, well recorded in Wyoming and surrounding basins, which decreases again in the Late Eocene, during which members of this group find refuge in California and Texas. Dental specializations allow the recognition of a number of tribes or subtribes, but a precise resolution of their phylogenetic relationships is difficult to achieve due to the large number of convergences in their dental characters. Rose et al. (1994, p. 20) summarized the problem thus: “Particular derived characters that must have evolved independently in two or more lineages include enlargement of I/1 (usually associated with crowding of anterior teeth), loss of one or more lower premolars, hypertrophy of P/4, molarization of P/4 (involving more distinct metaconid and paraconid or development of a talonid basin), reduction or enlargement of third molars, crenulation of enamel, and presence of a mesostyle”. In spite of these difficulties, added to an incomplete documentation of their early phases of divergence, successive phylogenetic analyses have recovered certain relationships, some of which are becoming consensual and will be mentioned below (Szalay 1976; Honey 1990; Gunnell 1995a; Muldoon and Gunnell 2002; Tornow 2008).

The record is extremely irregular, including taxa represented by one specimen as well as taxa represented by hundreds of them, and covering long time spans and large geographic areas.

Steinius, Omomys, Diablomomys, and *Chumashius*

These taxa constitute a first group. *Steinius verspertinus* is found in the Early Eocene of Wyoming. It is very primitive in retaining four premolars, a canine relatively as large as in *Teilhardina*, tall P/3 and P/4, and an unreduced P/3. Its sole clearly derived feature is a moderately enlarged I/1. If its unreduced M/3 and the more peripheral cusps on its molars were considered primitive relative to *Teilhardina*, it would imply the existence of an unknown lineage in the Earliest Eocene (Rose et al. 1994). The two latter characters make it a good candidate as an ancestral omomyine. In fact, a second species *S. annectens* is closer to *Omomys* and confirms the proximity of the two genera (Bown and Rose 1991).

The genus *Omomys* was described by Leidy in 1869. The species *O. carteri* is very abundant in Middle Eocene beds of the western regions of North America, accounting for 64–90 % of all omomyid specimens through the Early and Middle Bridgerian (Muldoon and Gunnell 2002). Its dentition is remarkably generalized in comparison with all other omomyines (Fig. 16). It has a moderately enlarged I/1, a

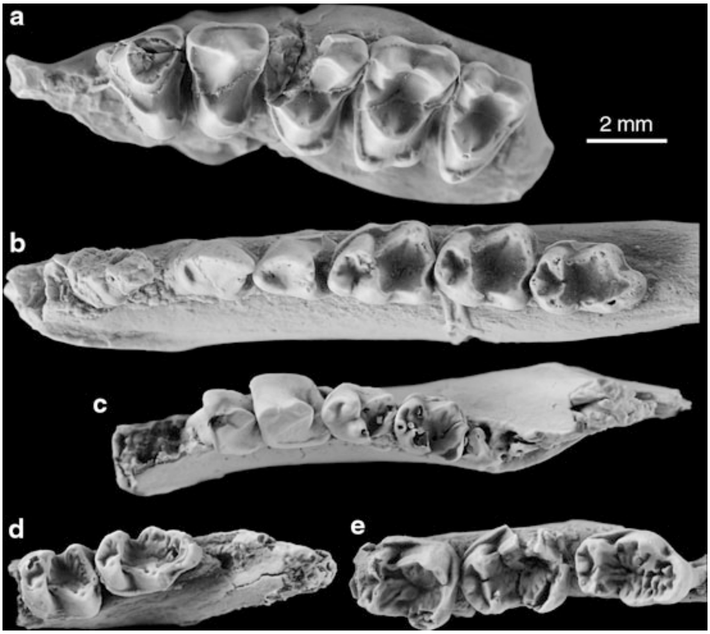

Fig. 16 Dentitions of omomyines, *Omomys, Uintanius*, and two utahiini, *Utahia* and *Stockia*. Maxilla (**a**) and mandible (**b**) of *Omomys carteri* showing a relatively primitive dentition. The right mandible of *Uintanius* shows a very enlarged P/4 (**c**). The molars of *Utahia kayi* (**d**) and *Stockia powayensis* (**e**) are derived through their short trigonid with a reduced paraconid and large crenulated talonid basins. Photographs of white-coated epoxy casts, all at the same scale

relatively small canine (smaller than I/1 and P/3), and a very small single-rooted P/2. P/3 and P/4 are relatively high and elongated; P/3 is simple and its short talonid is somewhat crowded below the anterior part of P/4. P/4 has a small metaconid. The three lower molars are simple with peripheral cusps and sharp crests. M/3 is unreduced. The paraconid is large and lingual on M/1, smaller and more labial on M/2 and M/3. P2/ is also very reduced. P3/ and P4/ have a large paracone, a parastyle, a lower protocone lobe with a preprotocrista, and a postprotocrista continuous with the complete posterior cingulum. The upper molars have a relatively broad (anteroposteriorly) trigon basin and no protocone fold. Both conules have their pre- and postcristae, and there are a hypoparacrista and a hypometacrista. The lingual cingulum is complete; a hypocone is present posteriorly, and a small pericone anteriorly on M2/. Detailed analysis of large assemblages of *O. carteri* from the Bridger Basin revealed aspects of intraspecific variability in dental traits (e.g., P/4 metaconid present in 91 % of individuals, M2/ pericones present in 80 %) and an increase in the frequency of several premolar features, suggesting anagenetic change through time (Cuozzo 2008). Three petrosals of *O. carteri* were analyzed in detail, revealing a series of characters of the otic capsule and middle ear cavity (Ross and Covert 2000). Most characters conform to an omomyiform model as documented in *Necrolemur* and *Shoshonius*, with minor differences between them. Postcranials of *O. carteri*, which are analyzed below, allowed an estimation of its body weight at 230 g (between 170 and 290 g; Anemone and Covert 2000).

A smaller species *O. lloydi* is documented in the early Middle Eocene. *Diablomomys dalquesti* is based on a maxilla from the Middle Eocene (Late Unintan) from Texas. Its M1/ is narrower lingually and has larger conules than in *Omomys*, and it has no lingual cingulum (Williams and Kirk 2008). *Chumashius balchi*, represented by a small number of specimens from California, is very close to *Omomys*. It differs from the latter only by its relatively larger canine, lower P/3 and P/4, and lack of distinct pericones and hypocones on the upper molars.

Uintanius and *Jemezius*

These form a small group of three species, sometimes considered close to *Omomys*, found to be a primitive sister group of the washakiins by Tornow (2008). *Uintanius* is characterized by enlarged P/3 and very enlarged P/4, which are exodaenodont: their enamel is ventrally extended below the alveolar margin on the labial side (Fig. 16). The upper premolars are also enlarged and have a reduced protocone lobe. The molars are relatively simple, the uppers having a small protocone fold. Alveoli of the anterior teeth preserved on a dentary of *U.* cf *rutherfurdi* show that *Uintanius* had two small subequal incisors, and a somewhat larger canine and P/2 (Gunnell 1995a). Szalay (1976) postulated that *Uintanius* specialized in food items which required great force to open but not much mastication. Gunnell found confirmation of this claim in a high proportion of dental specimens that showed heavy wear or had been broken and polished during life. *Jemezius szalayi*, found in the Early Eocene of New Mexico, has a lower and more complex P/4, relatively larger P3/ and P4/ protocones, and a relatively larger M/3 with a less compressed trigonid – characters which put it closer to *Steinius*.

Utahiini

A tribe Utahiini can be used to unite *Utahia, Stockia, Ourayia, Chipetaia, Asiomomys, Wyomomys*, and *Ageitodendron* (equivalent to the Ourayiini of Gunnell 1995a; Gunnell and Rose 2002). With the exception of *Ourayia*, known by two species (three specimens for each), all of these genera are monospecific and known essentially by (sometimes very limited) dental remains. They are all found in Middle Eocene beds, and *Utahia kayi* starts in the late Early Eocene of Wyoming. *Utahia, Stockia*, and *Chipetaia* have lower molars with large talonid basins, as well as compressed trigonids with reduced paraconids on M/2–3 (Fig. 16). The lower molars of *Chipetaia* are low and heavily crenulated (convergent with *Microchoerus*), reminiscent of frugivores with emphasis on seeds (Rasmussen 1996). *Asiomomys changbaicus*, from the Middle Eocene of northeastern China, known by one mandible bearing P/3 and M/2–3, is believed to be close enough to *Stockia* to testify to an utahiin dispersal from North America to China during the Middle Eocene (Beard and Wang 1991). The molars of *Asiomomys* are also partially convergent with those of the European *Nannopithex*, which does not imply close affinity but recalls how pervasive convergent characters can be. Gunnell (1995a) proposed a morphocline from *Wyomomys bridgeri*, which shows rounded simple talonids with robust labially bulging ectocingulid on M/2–3, without a talonid notch as found in *Utahia*, and with paraconid and metaconid isolated by a deep fissure; to *Ageitodendron matthewi*, which has a more reduced paraconid; to *Ourayia uintensis*, which has a more compressed trigonid without paraconid. More complete material from all these taxa is needed to more securely establish their relationships. Fragmentary hindlimb bones of *Ouraya* and *Chipetaia* are relatively similar to those of *Omomys* and *Hemiacodon*, which are detailed below (Dunn et al. 2006). Features such as the cylindrical shape of the femoral head in *Chipetaia* and details of the tibial plateau in *Ourayia* reflect a relatively large amount of leaping in these mid-sized primates. Body weight estimates are 500–700 g for *C. lamporea*, and 1,500–2,000 g for *O. uintensis* (Dunn et al. 2006).

Macrotarsiini

A tribe Macrotarsiini is used sensu Gunnell and Rose (2002) to unite *Macrotarsius, Hemiacodon*, and *Yaquius*, and to also include *Tarka, Tarkadectes*, and *Tarkops*, which have recently been shown to be closely related (Ni et al. 2010). *Hemiacodon* is a well-known genus described by Marsh, known by postcranials (Simpson 1940) and beautifully described by Szalay (1976, including a frontal). Gunnell mentioned 370 specimens of *H. gracilis*, from 50 different localities, in the collections of the University of Michigan. Yet its phylogenetic affinities have been debated (Fig. 17). It shares many dental characters with the washakiins, with which it was classified, with doubt, by

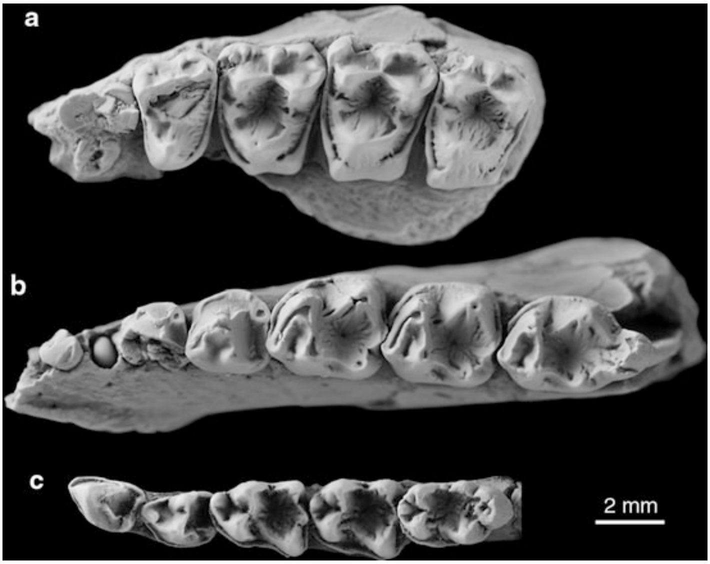

Fig. 17 *Macrotarsius* and *Hemiacodon*. Upper dentition of *Macrotarsius* showing the prominent molar mesostyle (**a**) and right mandible of *M. montanus* (**b**). Left mandible of *Hemiacodon gracilis* showing its P/4 with a well-formed trigonid (**c**). Photographs of white-coated epoxy casts, all at the same scale

Szalay (1976). It was taken out of the washakiins by Honey (1990), who emphasized that *Hemiacodon* has a greatly enlarged I/1 relative to I/2, more elongated and narrow (primitive) P/3–4, and a P/3 higher than P/4, whereas the known I/1–2 in washakiins are subequal in size and small, and their P/3 is slightly molarized, bearing incipient paraconid and metaconid. A different classification implies that *Hemiacodon* evolved enlarged conules, hypocones, and pericones in parallel with some washakiins. Honey hypothesized a sister group relationship with an extended concept of omomyini, including *Macrotarsius*, and Gunnell (1995a) restricted this close relationship to *Macrotarsius* only, a choice preserved by Gunnell and Rose (2002). *Hemiacodon* is found sister to a clade (*Macrotarsius* + Utahiins) by Tornow (2008). The upper molars of *H. gracilis* are more transversely elongated than in *Macrotarsius*; they have a protocone fold, large conules, rugose enamel, and a hypocone more distinct than in *Macrotarsius*. In the lower dentition, the P/4 is molarized, with a lingually arching paracristid and a well-formed and short talonid. The lower molars have peripheral cusps and high crests, and M/1–2 have a very wide talonid basin and distinct hypoconulids. The putative earlier species *H. casamissus*, represented by dentary fragments and worn molars, is considered doubtful. A new late Middle Eocene species, *H. engardae*, is larger and shows more acute crests on its lower molars and P/4, suggesting a probable increase in folivory (Murphey and Dunn 2009). *Hemiacodon gracilis* has long been the postcranially best-known omomyid. Its bones are analyzed below.

Five species of *Marcrotarsius* have been named. This genus has a wide geographic distribution, being found in Middle and Late Eocene beds of the western interior basins, Texas, California, Canada, and possibly also in China. The most primitive species, *M. jepseni*, is known by two dentaries and the palate of one individual. *M. montanus* has reduced lower premolars and especially small canines relative to its molars. Upper molars have an anteroposteriorly wide trigon, no hypocone or protocone fold, big mesostyles linked to the centrocrista, big parastyles, and a thick crenulated labial cingulum (Fig. 17). The lower molars are unusual in possessing a prominent crest posteriorly joining the metaconid to the entoconid. The species *M. macrorhysis* is based on two isolated teeth from the Middle Eocene Shanghuang fissure fillings of Jiangsu Province, China (Beard et al. 1994). These P/4 and M/1 are similar to those of *Macrotarsius* species; however, given the high number of dental convergences among omomyiforms, it would be important to have more complete evidence to confirm this generic attribution and its consequences for dispersals.

Three dentally specialized Middle Eocene genera are united in a subtribe or tribe Tarkadectini. Because they appear firmly rooted in species of *Macrotarsius* in the phylogenetic analysis of Ni et al. (2010), they are included here in the Marcrotarsiini. *Tarka stylifera* (Ui1) and *Tarkadectes montanensis* (Ui) were enigmatic species from the late Middle Eocene of Wyoming and Montana, often referred to the Plagiomenidae (Dermoptera) due to their broad lower molars bearing supplementary cuspules and upper molars with a wide stylar shelf and complex stylar cusps. The discovery of a more complete dentary in a Middle Eocene locality of Inner Mongolia, pertaining to a slightly less derived species named *Tarkops mckennai*, showed the anterior dentition to be typical of omomyids and unlike plagiomenids (Ni et al. 2010). At the same time, it illustrated another example of Middle Eocene dispersal between North America and Asia. The alveoli in front of the dentary of *T. mckennai* show that there was a large anteriorly inclined I/1, a small I/2, a larger vertical canine, a tiny P/2, and a two-rooted P/3. P/4 has a large metaconid, almost as high and anterior as the protoconid, and a smaller and lower paraconid. The lower molars are very bunodont; they have a shallow crenulated talonid basin, a long postmetacristid, and a peculiar cingular cusp at the labial base of the protoconid. *Tarka* and *Tarkadectes* have exaggerated the transversal breadth of their lower molars, which are endowed with supplementary cuspules.

Washakiini

This is one of the most interesting tribes of the omomyines. It includes 10 species, contained in the genera *Loveina, Basius, Shoshonius, Washakius* (4 species) and *Dyseolemur* (Fig. 18). They are known from the late Early and Middle Eocene, and *Dyseolemur* survives in the Late Eocene of California. They have transversely elongated upper molars with conules and a protocone fold. They tend to develop a moderately sized hypocone (*Washakius*) or a big mesostyle (*Shoshonius*). Their P/3–4 are moderate in size and slightly molarized. The P/4 paraconid and metaconid are well developed in *Washakius*. Their lower molars have a relatively transversely narrow trigonid. They develop a metastylid on the lower molars,

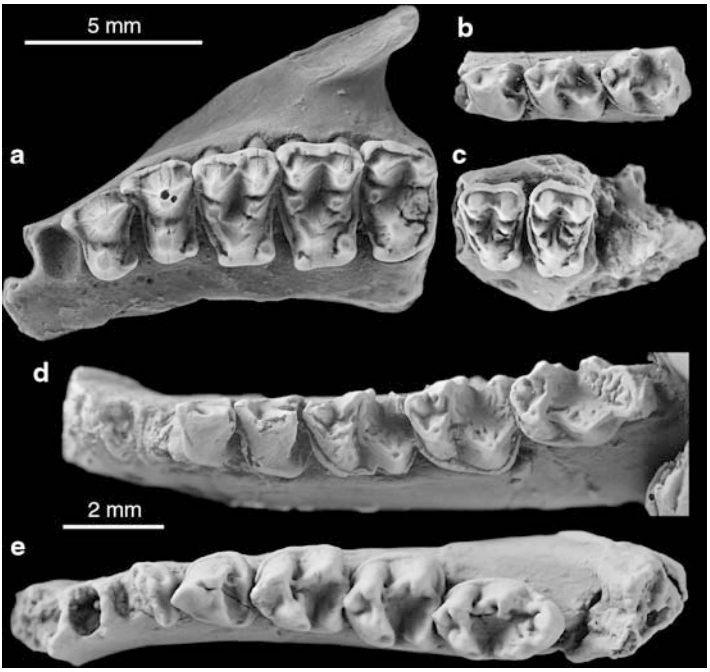

Fig. 18 Dentitions of Washakiini. Maxilla with upper teeth (**a**) and left mandible with P/4-M/2 (**b**) of *Washakius insignis* and fragmentary maxilla with M1-2/of *W. woodringi* (**c**), all at the same scale. Left mandible of *Shoshonius cooperi* (**d**) and right mandible of *Dyseolemur pacificus* (**e**), both at a similar scale, larger than for (**a**–**c**). Increase in cusp number is easily seen on the upper molars (**a** and **c**), and a metastylid behind the metaconid can be seen on the lower molars in (**d**) and (**e**). Photographs of white-coated epoxy casts

considered to be homologous between *Shoshonius, Washakius*, and *Dyseolemur*. They all have an elongated M/3. *Loveina* is the most primitive genus, starting with the rare and small *L. minuta* (Lisyte). Honey (1990) described two primitive species which extended the range of two separate lineages. *Shoshonius bowni*, more primitive than *S. cooperi*, was included in *Shoshonius* because it possesses enlarged mesostyles on its upper molars (convergent with *Ourayia* and *Macrotarsius*). *Washakius izetti* completed a morphocline *W. izetti – woodringi – insignis*, tracking a progressive enlargement of pericone and hypocone, as well as an increase in size of the metastylid. This morphocline in fact includes two lineages, and *W. woodringi* is clearly ancestral to *Dyseolemur*.

The washakiins have received renewed attention since the discovery of several partial crania and postcranials of *Shoshonius cooperi* in the late Early Eocene of the Wind River Basin, Wyoming (Beard et al. 1991; Beard and MacPhee 1994; Dagosto et al. 1999). The crania possess very large orbits, which not only indicate probable nocturnality but also raise the issue of a possible relationship with tarsiids. A detailed analysis of available cranial characters led to the conclusion that *Shoshonius*, *Tetonius, Necrolemur*, and *Tarsius* pertained to a monophyletic taxon, Tarsiiformes (Beard and MacPhee 1994). They share a series of derived characters: posteromedial and anterolateral bony flanges that overlap the bulla, narrow, peaked choanae, a narrow central stem of basicranium, reduced snout, parotic fissure, and suprameatal foramen. The authors add that, among the fossil tarsiiforms known by relatively complete cranial remains, *Shoshonius* appears to share the most recent common ancestry with *Tarsius*. They refrain from referring the washakiins to Tarsiidae because the phylogenetic relationships between washakiins and other omomyine tribes are not clearly resolved. In fact, several of the listed characters might be consequences of small size and large orbits as much as common heritage. Information from more omomyid genera is needed to further evaluate these characters. In the recent description of *Archicebus, Necrolemur* is said to have a non-reduced snout (Ni et al. 2013). Furthermore, *Necrolemur* has also been cited as possessing anatomical strepsirhinism. The monophyly of a broad tarsiiform clade comprising tarsiids, omomyids, and michrochoerids implies the convergent evolution of anatomical haplorhinism in tarsiiforms and simians, which would destroy the basis for the concept of Haplorhini (based on tarsiids + anthropoideans, see below). Such a far-reaching conclusion needs to be carefully evaluated. The postcranials of *Shoshonius* are analyzed below with those of other omomyines. When the postcranial characters were added to the cranial characters used in the phylogenetic analysis described above, tarsiiform monophyly was again recovered, but this time with *Necrolemur* as the sister group of *Tarsius* instead of *Shoshonius* (Dagosto et al. 1999). Adding the dental evidence would not clarify the issue, as *Tarsius* can hardly be rooted in the microchoerids, most of which have a very distinctive dental formula, and it is not any easier to root the dentition of *Tarsius* in the washakiin dentition (or the reverse). If there are phylogenetic relationships, they are not close. The phylogenetic relationships of *Tarsius* are further considered below.

The postcranial anatomy of the omomyines is progressively better documented, and its interpretation in terms of locomotor behavior has been correlatively enhanced. For a long time the limb bones of *Hemiacodon gracilis* were the best documents. Several bones were found together, including a partial pelvis, femoral and tibial extremities, and a partial right foot with astragalus, calcaneum, cuboid, navicular, entocuneiform, and first metatarsal (Simpson 1940; Szalay 1976). Their functional interpretation progressively improved (e.g., Dagosto 1985, 1993; Gebo 1988). Postcranials of two other omomyines were subsequently found and described at almost the same time: those of *Shoshonius cooperi* (Dagosto et al. 1999) and those of *Omomys carteri* (Anemone and Covert 2000). Because the bones in common between these taxa show an overall similarity, they are described and analyzed jointly here. The lower limb is the best documented, and it shows clear signs of leaping adaptation. A complete femur is known only for *Shoshonius*, in which it appears relatively short and robust. The proximal femur has an overall similarity in the three genera, bearing a semicylindrical articular surface on its head and a short neck forming an angle of more than 90° with the shaft. The articulation of the head is more cylindrical and the neck angle close to 90° in living specialized leapers. The morphology of the knee joint particularly well reflects its

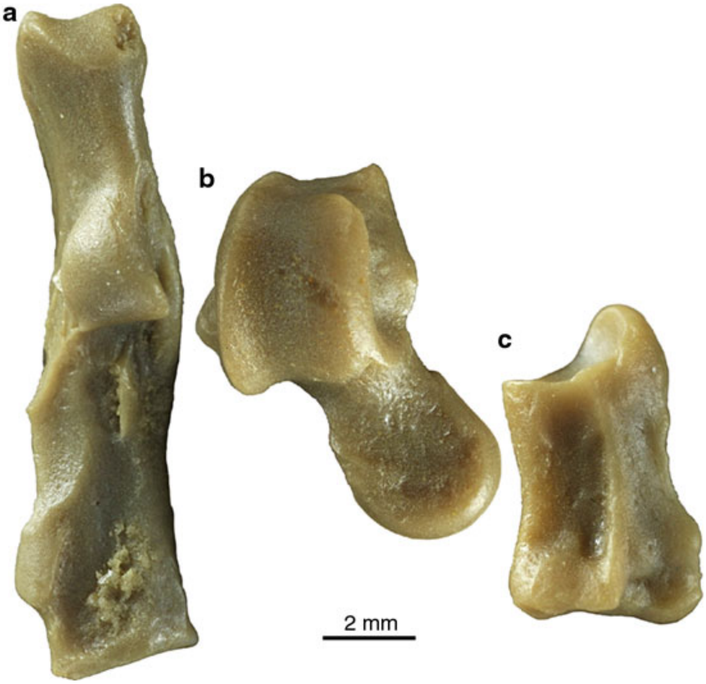

Fig. 19 Three foot bones of *Omomys carteri*. Calcaneum (**a**), astragalus (**b**), and navicular (**c**), all in dorsal view. The calcaneum shows the two articular facets on which the astragalus lies and a marked distal elongation (and small artifacts of casting). The astragalus shows the long and salient lateral rim of the tibial trochlea. The well-grooved trochlea and calcaneal and navicular elongation are interpreted as reflecting a moderate leaping adaptation

function. The three genera have a distal femur with an anteroposteriorly very high distum, a deep patellar groove bordered by a prominent lateral ridge. The femoral condylar index of 111 in *Omomys* and 119 in *Hemiacodon* (111.5 in *Shoshonius* for a close index) is similar to that of specialized leapers. *Omomys* has a retroflexed tibial plateau and a mediolaterally compressed proximal shaft. All of these characters are typical of specialized leapers, implying that powerful leaping was a component of the locomotor repertoire in these genera (Anemone and Covert 2000). The distal tibia shows an extensive distal articulation between tibia and fibula, which prevents rotation and is found in leaping primates. It seems that this articular surface is more extensive in *Shoshonius* (around 25–35 % of tibial length; Dagosto et al. 1999) than in *Omomys*. Concerning foot bones, the three genera have very similar calcanea (also quite similar to those of *Teilhardina*) (Fig. 19). They all show a moderate elongation of their anterior part (anterior length/total length is 51 % in *Shoshonius*, 51.4 % in *Omomys*, 52 % in *Hemiacodon*; also 53 % in *Washakius insignis*, Gebo 1988). Their astragali as well are similar to each other and to those of other omomyines: high and narrow trochlea, long neck, spherical head (not in *Hemiacodon*), no posterior trochlear shelf. The navicular is moderately elongated, as is the calcaneum, which is similarly the case for both in living cheirogaleids. However, in *Hemiacodon* and *Omomys* there are also a cuboid and an entocuneiform which are more elongated than in living primates. Elongation of the foot is another indication of leaping; however, the foot of these omomyines is not as extremely elongated as in the living specialized leapers. There is a screw-like articulation between astragalus and calcaneum, and a pivot joint between calcaneum and cuboid, allowing for some rotation of the foot. Both the entocuneiform and its sellar articular facet, and the first metatarsal with its enormous peroneal tubercle (long, tall, mediolaterally narrow), reflect a foot with powerful hallucial grasping. The pelvis, partially known in *Hemiacodon* and *Omomys*, reveals in the latter a shorter ilium and a longer ischium than in living prosimians. The ischium is also less dorsally expanded than in leaping prosimians. These proportions might be more primitive (they recall tree shrews) and/or indicative of a more generalized form of leaping than in living leapers, using horizontal and oblique supports more than vertical ones (Anemone and Covert 2000).

The forelimb is less well documented. A complete humerus is known only in *Shoshonius*. It has a relatively round head, strongly developed attachment areas for the shoulder muscles, and a prominent brachial flange. The trochlea is long and low. The elbow joint, like the shoulder joint, is that of a quadruped and leaper (Dagosto et al. 1999). The presence of a complete humerus and femur allows an estimation of the humero-femoral index at 64.6 for *Shoshonius* (and of an intermembral index probably between 64 and 68). Most of these anatomical characters suggest that these omomyines were similar in their locomotor repertoire to cheirogaleids or to the more frequently quadrupedal galagos (*Otolemur, Galagoides*). They probably used powerful leaping, although quadrupedalism and climbing were also important parts of their locomotor repertoire. There are certainly more small differences between them than the few mentioned above, and more precise interpretations in terms of frequencies of behavior or support use are difficult to obtain (Dagosto 1993). The deep slope on the fibular side of the astragalus and the moderate medial rotation of the tibial malleolus indicate that dorsiflexion of the foot was accompanied by only a slight degree of abduction of the foot, contrary to what is observed in strepsirhines (Dagosto 1985).

European Microchoeridae

The European Microchoeridae are numerous enough to deserve recognition as a family. They had long been suspected to be rooted in the Earliest Eocene *Teilhardina belgica*; this hypothesis received a recent confirmation through the discovery of two Early Eocene intermediate species, of the genus *Melaneremia*. *M. schrevei* is the older and more primitive (Hooker 2012). Compared to *T. belgica*, it shows a lowering of the protoconid of P/4, more accentuated on P/3, a broadening of P/4, especially of its posterior part, and a more developed paraconid and metaconid on that tooth, more developed cingulids on the lower molars, a marked broadening of the M/3 talonid basin and third lobe, and incipient modifications of the M/2–3 trigonid. The younger *M. bryanti* has a more reduced P/3 (Hooker 2007). These species provide a link with the genus *Nannopithex*, which is known through many species in the late Early and Middle Eocene. Two crushed crania and several almost complete lower jaws are known in species found in the Lutetian lignite mines of the Geiseltal, Germany. They show that these species had a very enlarged lower anterior incisor, followed by a reduced I/2, a canine, and two premolars. Compression of the teeth located between I/1 and P/4 led to the loss of P/2 and the reduction of P/3, which is single-rooted. The resulting dental formula, 2123 for lower teeth, will remain stable in later microchoerids. In the upper dentition, I1/ is enlarged, followed by a smaller I2/ and a larger canine; in some of these *Nannopithex* P2/ is lost, whereas it will still be present in later necrolemurines. The oldest species, the late Early Eocene *N. zuccolae*, shows a number of characters typical of *Nannopithex*: enlarged P/4 with ventrally expanded enamel on its labial side, very small metaconid and curved paracristid without paraconid; lower molars with trigonid becoming narrower on M/2–3, smaller paraconid slightly labial and joined to the metaconid summit by a crest; large M/3 talonid basin posteriorly extended in the broad third lobe, and some enamel wrinkling. On the upper teeth, P4/ appears transversely extensive (as much as M1/), with a protocone lobe slightly narrower than the labial part and a low protocone. The upper molars have small conules, with a postmetaconule-crista joining the metaconid summit, whereas a postparaconule-crista is only variably present; there is no lingual cingulum or hypocone, and a protocone fold is variably present. Among evolutionary tendencies observed in *Nannopithex* species are a progressive broadening of the protocone lobe of P3/, on upper molars an increase in the size of the conules and development of supplementary crests on the walls of the trigon basin, strengthening and isolation of the protocone fold ("*Nannopithex*-fold"), and development of a small cingular hypocone on the posterior cingulum; on M/2, the paraconid continues to shrink into a continuous paralophid. These characters are best expressed in *N. filholi* from Lissieu, an MP 14 locality (Godinot et al. 1992). Three other species, *N. raabi, N. humilidens*, and *N. barnesi*, are known in the Geiseltal sequence (Thalmann 1994). The genus *Nannopithex* is probably a paraphyletic stem genus, in which most later clades of microchoerids originate.

The genus *Vectipithex* has been erected for three species known almost exclusively by isolated teeth (Hooker and Harrison 2008). They show that species phenetically close to *Nannopithex* survived in northern European localities until the Late Eocene, at a time when *Pseudoloris* and microchoerines were abundant in more southern regions. The oldest one, *V. quaylei* from Creechbarrow (Bartonian, MP 16), retains very large anterior incisors, a transversely broad P4/, and a P3/ with a small protocone lobe. It is advanced over *Nannopithex* through its M/1 without paraconid and its upper molars having an almost complete lingual cingulum with crestiform hypocone. M2/ is lingually narrow, whereas M1/ is broader in its lingual part. The Late Eocene *V. smithorum* is larger and has a lingually narrower P4/ and somewhat transversely shorter upper molars with slightly larger hypocones. The Late Eocene *V. ulmensis* from Ehrenstein in Germany is known by a few isolated teeth, which are again larger and have more massive proportions. In their

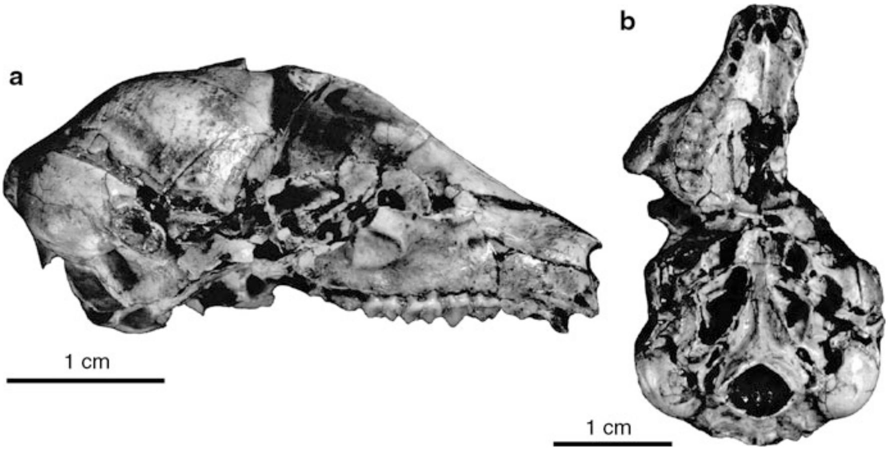

Fig. 20 One of the best-preserved crania of *Necrolemur antiquus* from the old Quercy collections (Montauban) in lateral (**a**) and ventral (**b**) views at two different scales. On the ventral side, the tympanic bullae have been prepared; their posterior extensions, or mastoid bullae, are preserved; anteriorly, alveoli show the presence of two well-separated and large anterior incisors. The lateral view shows that the muzzle of *Necrolemur* is anteriorly elongated

phylogenetic analysis, Hooker and Harrison (2008) find *Vectipithex* species to be rooted close to *N. raabi* and thus transfer the latter species into *Vectipithex*.

Species of *Necrolemur* and *Microchoerus* form a morphologically tight group, abundant in the late Middle and Late Eocene. The species *Necrolemur antiquus* has long been known by beautiful crania found in Quercy fissure fillings (Filhol 1874; Stehlin 1916). Its orbits are relatively large, an observation which was used to support tarsiiform affinities; however, these orbits are like those of living strepsirhines, and are interpreted as reflecting nocturnal habits. A posterior expansion of the auditory chambers is so large that it forms a "mastoid bulla" which is salient on each side on the back of the cranium (Fig. 20). The basicranium of *N. antiquus* was studied in detail by Szalay (1975). It has since served as one of the best-known references for omomyiform basicranial characters (see below on Haplorhini and tarsiid sister groups). *Necrolemur* differs from species of *Nannopithex* by more squared upper molars, especially M1/, linked to a larger cuspidate hypocone. It has crenulated molars and a duplicated metaconule. Lower molars have a trigonid which becomes shorter and transversely broader from M/1 to M/3. Contrary to *Nannopithex*, the M/3 is short with a reduced third lobe, and almost rectangular with trigonid and talonid of similar breadth. M/1 retains a large paraconid. A progressive increase in crenulation and upper molar lingual breadth can be observed from the primitive unnamed species of Egerkingen to intermediate forms from La Bouffie, to Late Eocene forms closer to the *N. antiquus* type specimen, which has stronger crenulation and a larger hypocone on M1/ and M2/ (Godinot 2003). Such a crenulated dentition has no analogue in living prosimians; it presumably suggests an adaptation to some kind of abrasive food. Postcranials of

Quercy *N. antiquus* include an elongated femur with high distal extremity, a fused distal tibia and fibula and an extremely elongated calcaneum, such as occur only in *Tarsius* among living primates, and an astragalus with a deeply grooved trochlea which was tightly maintained between the tibial and peroneal malleolae (Schlosser 1907; Godinot and Dagosto 1983). All of these characters typify an extreme leaping adaptation, unique until now in the Eocene fossil record, as is found in living forms which essentially move by long jumps between vertical supports (VCL). Vertical clinging is confirmed by the position of the foramen magnum below the cranium, visible in a larger *Necrolemur* skull.

Species of *Microchoerus* are essentially large *Necrolemur* with more crenulated enamel, which develop a mesostyle on their upper molars. Two species are known in the Bartonian locality of Creechbarrow, England (MP 16), *M. wardi* and *M. creechbarrowensis*. Hooker (1986) related these two species to the later occurring *M. erinaceus* (Hordle, MP 17a, England) and *M. edwardsi* from an unknown level in the Quercy region, which are also large, heavily crenulated, and display the most strongly molarized p/4 of all, with big and high metaconid and paraconid. However, the study of assemblages from Quercy in biochronological order revealed a continuous lineage, which increases in size and molar crenulation and develops a mesostyle. This lineage links a species of *Necrolemur* cf *antiquus* (stage of La Bouffie) to assemblages extremely close to *M. erinaceus* (Godinot 1985). These hypotheses will have to be restudied with quantitative approaches. There are convergences in the increasing molar crenulation of different lineages. This process culminates with the extraordinary *M. ornatus* described by Stehlin (1916), which has highly tuberculated upper teeth.

Species of *Pseudoloris* are small and developed pointed teeth, adapted to insectivory, which are convergent with those of *Tarsius*. However, the anterior dentition retains the stamp of the family, with moderately enlarged anterior incisors of typical morphology and single-rooted P/3 somewhat crowded under the P/4 (it probably lost the reduced I/2 of others). The muzzle of *Pseudoloris* shows proportionately large orbits, due to its small size, and this makes it even more similar to *Tarsius* (see discussion of tarsiid sister groups below). The best-known species is *P. parvulus* from the Quercy fissure fillings, which appears long-lived. Early assemblages from Le Bretou show lower molars with a relatively open trigonid, whereas later assemblages usually show them with a longer paracristid more or less closing the trigonid anteriorly. M/3 have a narrow third lobe. P/4 remains very simple, with only an incipient metaconid. Upper molars have a small paraconule and a well formed metaconule with well formed pre- and postmetaconule-cristae. There are small variations in the size of the hypocone, which in any case remains small. Larger species known by fragmentary remains are documented: *P. crusafonti* from Grisolles, France, and *P. reguanti* from Sant Cugat de Gavadons, Spain (Louis and Sudre 1975; Minwer-Barakat et al. 2013). New species of *Pseudoloris* have been described from Spain: *P. cuestai* and *P. pyrenaicus* (Minwer-Barakat et al. 2010, 2012). *P. cuestai* is typified by I/1 quite unlike those of other microchoerids, which calls for further analysis. One species, *P. godinoti*, has been demonstrated to have survived the Late Eocene climatic deterioration, being present in the lower Oligocene of Spain (Köhler and Moyà-Solà 1999). The oldest species sometimes referred to *Pseudoloris* deserve to be placed in a different genus, *Pivetonia*, with *P. isabenae* known in Spain and *P. saalae* known in the Geiseltal (Thalmann 1994). These very small species are phenetically closer to *Nannopithex* species, suggesting a rooting of the *Pseudoloris* group as well in the stem genus *Nannopithex*. *Pseudoloris* has been mentioned in the Late Eocene of Nei Mongol (Wang 2008), but the lower molar referred to *"P. erenensis"* is too different from the European genus. It belongs to another taxon.

The species *Paraloris bavaricus* has been found in Late Eocene marine sediments. Its lower jaw with four teeth shows a unique combination of characters: posteriorly narrowing P/4 without metaconid, smooth enamel on lower molars, M/1 with moderate-sized paraconid, relatively short paracristid on M/2–3 (Fahlbusch 1995). It is unlike all other genera, possibly due to branching very early (before *Melaneremia* for Hooker and Harrison 2008). It shows that undocumented lineages existed in unsampled regions of Europe, e.g., towards the east.

Possible Asiatic Omomyiforms

Other omomyiforms have been described in Asia. The existence of *Teilhardina asiatica*, described above with other species of *Teilhardina*, underlines the fact that a diversification of omomyiforms in Asia can be expected. However, several species are known only by very fragmentary remains. These were first compared with European and North American taxa, but they most probably document Asiatic groups. *Baataromomys* is known by one lower molar from the Early Eocene of Inner Mongolia, close to that of a *Teilhardina* (Ni et al. 2007). As mentioned above, "*Pseudoloris*" *erenensis* from younger Eocene strata of the same country is not a microchoerid (Wang 2008). Is it an omomyiform, or an eosimiid? *Vastanomys*, from the Early Eocene Vastan mine in India, has an omomyid-like M/2; but a referred upper molar, transversely elongated, is also reminiscent of eosimiids (Bajpai et al. 2005). More material is eagerly awaited. Among several species from the late Early Eocene of Pakistan, *Kohatius* is known by isolated M/1 and P/4, and *Indusius* by isolated M2/ and M/2 which are somewhat reminiscent of microchoerids (Russell and Gingerich 1987; Gunnell et al. 2008). These fragmentary fossils confirm that a vast proportion of Eocene Asiatic primates, particularly the omomyiforms, are still unknown.

The Early Eocene *Altanius* from Mongolia is better documented. It is an extremely small species, with the primitive dental formula of 2143 below and probably above (Fig. 21). Alveoli show a canine larger than the two small incisors below, and larger than the anterior premolars above and below. P/4 through M/3 are superficially omomyid-like, but their protoconids have extended labial slopes, especially on M/1, which recall plesiadapiforms. Its upper molars are transversely extended and bear well-formed para- and metaconules. Their crown is very high in labial view, and a strong protocone fold is added to the protocristae (i.e., not derived from the postprotocrista as in omomyids), contributing to its plesiadapiform stamp. Despite being described as a primitive

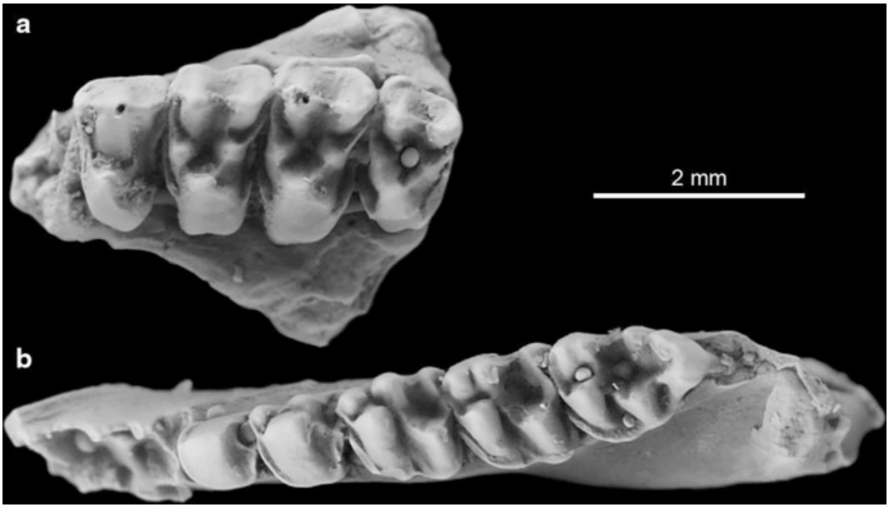

Fig. 21 *Altanius orlovi* from the Early Eocene of Mongolia, upper (**a**) and lower dentition (**b**): it is a very tiny species. Photographs of white-coated epoxy casts, both at the same scale

omomyid (Dashzeveg and McKenna 1977) and considered an anaptomorphine by Szalay and Delson (1979), its affinities are probably closer to plesiadapiforms than to the earliest primates (Rose and Krause 1984). If it were a primate, it would contribute critical information to the reconstruction of their primitive dental morphotype. A better understanding of its dental adaptation and affinities would be welcome.

Tarsiidae, Possible Tarsiiformes, and the Concept of Haplorhini

The Concept of Haplorhini

Among living primates, shared derived characters of soft anatomy, reproductive organs, and genetic markers unite tarsiids and simians in a monophyletic clade Haplorhini. The name comes from characters of the nose and face: tarsiers and simians have lost the moist rhinarium typical of strepsirhines and other mammals, and replaced it with dry and hairy skin. Anatomists have looked for osteological characters, which would allow the recognition of fossil haplorhines. The most attractive of them, the presence of a postorbital septum isolating the eye from the temporal cavity, has turned out to be problematic. The orbital wall of simians consists of the frontal, alisphenoid, and a large zygomatic, whereas that of tarsiers consists of the frontal, alisphenoid, a small zygomatic, and a large amount of maxillary bone. Because the constituents are not the same, some researchers have argued that the two septa must have evolved convergently (e.g., Simons and Russell 1960; Simons and Rasmussen 1989), whereas others have argued that sutures can move through time, and that a zygomatic-alisphenoid contact is so exceptional that it must be at least partly homologous (e.g., Cartmill 1980). Recent embryological work concerning the septum shows that of tarsiers to be formed by a processus different from that of simians: no frontal spur, and ossification of a membrane (Smith et al. 2013). This seems to support the convergence hypothesis, even though some paleontological confirmation would be welcome to eliminate any kind of common precursor morphology. In any case, detailed anatomical work has found other derived anatomical characters supporting a clade (*Tarsius* + simians) in the basicranium, a region which has provided characters linked to higher systematic categories. MacPhee and Cartmill (1986) provided six such characters from the otic region, which subsequently have been elaborated (Ross 1994; Ross and Covert 2000). Agreed upon are the presence of a septum isolating an anterior tympanic accessory cavity, the anteromedial location of the posterior carotid foramen, the perbullar carotid pathway (through the petrosal septum), the extrabullar ventral edge of the tympanic bone (no annular bridge), and a highly reduced or absent stapedial artery.

To the above list can be added characters more or less directly dependent of anatomical haplorhinism. The absence of an interincisor diastema, between the roots of the two I1/, is correlated with the loss of the rhinarium, which requires such a space for its philtrum (Beard 1988). Haplorhinism had been correlated with a smaller infraorbital foramen indicative of a reduction of the sensory organs of the muzzle, the vibrissae (Kay and Cartmill 1977). However, this has recently been refuted in favor of a different adaptive meaning, related to diet (Muchlinski 2010a). Haplorhinism is likely correlated with an abbreviated snout, and some reduction of the nasal cavity and olfactory organs. Linked to this is a reorientation of the nasolacrimal canal, which is anteriorly inclined in strepsirhines, and shorter and vertical in haplorhines. A detailed embryological study showed that the vertical canal and duct in tarsiers and simians is acquired by exactly similar embryological processes, giving a strong argument in favor of their homology, and of a monophyletic Haplorhini (Rossie and Smith 2007).

The whole process of the acquisition of anatomical haplorhinism may have been driven by an emphasis on vision in the lineage leading to haplorhines. Tarsiers and simians possess a fovea in their retina, which considerably increases visual acuity. They also lack the tapetum lucidum, a reflecting membrane behind the retina which enhances vision in low levels of light and is present in living nocturnal strepsirhines. This lack explains why tarsiers possess such enormous eyes, larger than those of other nocturnal prosimians. Some of the peculiar cranial characters of tarsiers are probably related to these enormous eyes, starting with their postorbital septum. The fovea in the eye was probably acquired to enhance vision in diurnal species. Hence the early haplorhines can be reconstructed as diurnal, possessing relatively small orbits (Cartmill 1980). *Tarsius* became secondarily nocturnal and in the process acquired its enormous eyes and other autapomorphies.

The preceding list of characters strongly supports a clade Haplorhini, based on the derived characters shared by tarsiers and anthropoids, even if some of them turn out to be difficult to use (e.g., the quantitative ones) or include partial homoplasy. However, these numerous characters were acquired sequentially, and fossil evidence will be needed to decipher in what order. Some characters used to define haplorhines in the past now appear problematic; for example, the apical passage of the olfactory nerves above an interorbital septum was thought to characterize a more inclusive group (omomyiforms + crown haplorhines) until it was found lacking in the simiiform *Aegyptopithecus* (Simons and Rasmussen 1989). Because known omomyids lack most of the above-listed characters, it is unwise to extend to them a definition of haplorhines, which would thereby lose its content. Alternatively, if the washakiins can be shown to share enough of these characters, they might be included in tarsiiforms and character-based haplorhines. An alternative view is supported by those who propose a sister group relationship between some omomyiforms and *Tarsius*. Such a view implies that anatomical haplorhinism was acquired convergently in tarsiids and anthropoideans – an unparsimonious assumption, which would require grounding in a convincing fossil record, or else refutation of the homologies listed above. This discussion will be picked up again in section "Proposed Sister Groups for Tarsiids" below.

Fossil Tarsiidae

The family Tarsiidae has long been absent from the Paleogene fossil record. However, the discovery of teeth extremely similar to those of the living tarsier led to the description of *Tarsius eocaenus* in the Middle Eocene fissure fillings from Shanghuang, China (Beard et al. 1994). These five isolated cheek teeth were completed by the description of a piece of maxilla with P3/, coming from a different fissure but also very similar to the living *Tarsius* (Rossie et al. 2006). Specifically, this small specimen shows two similarities with *Tarsius*: a relatively reduced infraorbital foramen and a short vertical nasolacrimal duct. As seen above, the former is not as diagnostic as formerly believed; the latter, however, really seems to turn the specimen into an "anatomical haplorhine" (Rossie et al. 2006), i.e., a haplorhine in the sense used here. By contrast, contemporary omomyiforms appear markedly different.

Tarsal bones found in the Shanghuang fissure fillings have also been ascribed to tarsiids (Gebo et al. 2001). The calcaneum is distally incomplete; but it appears elongated in its distal part, and also progressively narrower distally, which makes it more similar to tarsiers than other Shanghuang calcanea (see Fig. 35). An astragalus is similar to that of *Tarsius* in its wide body bearing a wedge-shaped trochlea, a short neck, and a low neck angle. Many of these characters suggest a marked leaping adaptation. However, the astragalus also has a small trochlear shelf, whereas *Tarsius* is lacking such a shelf. Some other differences with *Tarsius* led the authors to conclude that these tarsals belong to a genus other than *Tarsius* (Gebo et al. 2001). Possibly Shanghuang dental tarsiids shared the nocturnal adaptation of *Tarsius* and associated anatomical characters, but not yet the full vertical clinging and leaping (VCL) specialization of living tarsiers.

Another Middle Eocene genus found in the Heti Formation of the Yuanqu Basin (Shanxi Province, China) has been ascribed to the tarsiids. *Xanthorhysis tabrumi* is represented by a tiny lower jaw bearing P/3–M/3 and alveoli for a P/2 and a larger canine (Beard 1998). P/3 and P/4 have a pointed protoconid and a very simple and reduced talonid. P/4 has a small metaconid, a weak and almost complete labial cingulid, and a thicker anterolingual cingulid. The lower molars are primitive in possessing a trigonid with strong paraconid. The trigonid is similar in M/1–M/3, as is typical of *Tarsius*. The talonid basin is broader than the trigonid, and the entoconid is well formed. M/3 has a very short third lobe, much smaller than in *Tarsius*, similar to that of *Eosimias* but more pinched. The dentition shows a striking overall similarity to that of *Eosimias*, a genus studied below.

Proposed Sister Groups for Tarsiids

Comparisons of small Eocene fossil primates with *Tarsius* have been conducted for a long time. At the beginning of the twentieth century several authors held the view that omomyids were not distinct enough to be placed in a different family, and they were thus ascribed to Tarsiidae (e.g. Matthew in Matthew and Granger 1915). However, there were dissenting views as well. Central to these discussions were the crania of *Tetonius* and *Necrolemur*. For example, Stehlin (1916) gives a detailed explanation of why he does not follow Gregory in placing *Necrolemur* in Tarsiidae, and why he prefers to maintain a family of “Necrolemuridae” (=Microchoeridae); he argues that *Necrolemur* and *Microchoerus* are dentally too specialized and thus follow a divergent evolutionary line (also shown by the mastoid inflation) – a point made earlier by Schlosser (1907). A revived defense of the close affinity of *Necrolemur* and *Tarsius* was put forth by Simons (1961), who nevertheless used the family “Necrolemuridae.” As seen above, the matter has become more complex in recent decades, with more omomyid crania discovered, tarsiids identified by the Middle Eocene, Eosimiidae entering these discussions (see below), and renewed anatomical research. Clearly, however, the view that tarsiids could be part of a monophyletic Tarsiiformes that includes a number of omomyiforms (and particularly microchoerids) stands in sharp opposition with the concept of Haplorhini as endorsed here. As seen above, it would imply the convergent acquisition of haplorhinism in tarsiiforms and simians, a far-reaching conclusion.

The two groups which continue to be central to this debate are the microchoerids with *Necrolemur* and *Pseudoloris*, and the washakiins with *Shoshonius*. The large orbits of *Necrolemur* have been emphasized, but they appear to be as in nocturnal strepsirhines of similar size, not tarsier-like. The characters linked to an extreme leaping specialization, reaching the stage of tibio-fibular fusion, also produce a list of shared derived characters that can lead to *Necrolemur* being the sister group of *Tarsius* in some parsimony analyses (Dagosto et al. 1999). However, as discussed long ago by Stehlin (1916), leaping specializations are numerous in primates, so that convergence is easily possible. The most powerful arguments in favor of the *Necrolemur*-tarsier hypothesis were reassessed by Rosenberger (1985), who added the peaked shape of the choanae, the pterygoid fossa encroached by the bulla, and recalled the significance of the extensive laminar contact between pterygoid and bulla, the shape of the guttered temporo-mandibular joint, and some less striking characters. These shared derived characters have been given as evidence in favor of close *Necrolemur*-tarsier phylogenetic relationships. However, as seen above, *Necrolemur* has anatomical strepsirhinism, a relatively long snout, and orbits of "normal" nocturnal size. Also, as emphasized by earlier authors, *Tarsius* is very unlikely to be derived from a species having the typical microchoerid dental formula; it possesses an anterior accessory auditory chamber, whereas the microchoerids developed their posterior mastoid inflation, demonstrating that they belong to two divergent phylogenetic lineages.

Pseudoloris plays a role in the debate because it shows additional similarities with *Tarsius* in dental traits linked to insectivory. Its position as sister group of *Tarsius* sometimes reappears in parsimony analyses of very large data sets (e.g., Ni et al. 2013). However, inasmuch as a position of *Tarsius* nested within microchoerids is impossible, this result shows that parsimony analyses can be driven by overall phenetic similarity, to the detriment of real phylogenetic affinities. Taxon sampling to date has not been complete enough to allow resolution of the debate. *Necrolemur* and *Pseudoloris* appear well inserted in the European microchoerid radiation, which has an almost continuous history going back to *Teilhardina belgica*, and in which the distinctive dental formula was acquired very early. They are unlikely to be sister group of tarsiids, but raise good questions concerning the acquisition of the above-mentioned synapomorphies: were these inherited from *Teilhardina* on, or did they converge under similar adaptive pressures (especially on vision)?

Another candidate for the sister taxon of *Tarsius* is the North American omomyine *Shoshonius* (Beard et al. 1991). After careful reevaluation of many cranial characters, Beard and MacPhee (1994) find a number of similarities shared with *Necrolemur* (presence of a parotic fissure) and other characters more specifically shared with *Tarsius* (e.g., enlarged orbits, abbreviated snout, narrower annular bridge). Furthermore, Rossie et al. (2006) briefly mention that *Shoshonius* possessed a vertical nasolacrimal canal, like *Tarsius*. This might make *Shoshonius* a real tarsiiform and character-based haplorhine, or it might be an argument in favor of convergent acquisition of haplorhinism. Then again, *Shoshonius* does not show the beginning of a postorbital closure similar to that of *Tarsius*, its dentition is not especially similar to that of tarsiids, and its postcranial characters are much less specialized for leaping than in tarsiids: their phylogenetic relationship cannot be very close. Also, such a relationship would call for an analysis of the washakiin tribe, in which all specialists place *Shoshonius*: are the washakiins well nested within the omomyine radiation? The omomyines seem to represent a relatively well-documented North American diversification, rooted in *Steinius*; the *Tarsius*–*Shoshonius* relationship would thus imply a North American origin for the tarsiids, which would have to be descended from a washakiin dispersal into Asia. Other omomyin tribes, when known, appear not to have acquired hypertrophied orbits and other characters linking them so closely to *Tarsius*. Another possible scenario is that the washakiins represent immigrants from Asia, pertaining to a group closely related to tarsiids. These scenarios need to be further explored and tested.

To conclude, if *Tarsius* were shown to be the sister group of more primitive omomyiforms, and not of early anthropoideans, this would imply the convergent acquisition of haplorhinism in the two groups. Haplorhinism would become an adaptive grade, reached by two lineages and more or less approached by others, under the adaptive emphasis on vision in small species (snout and nose reduction). Until now, the evidence does not appear sufficient to adopt this gradistic view, to the detriment of the haplorhine clade.

Archicebidae

For the recently described *Archicebus achilles*, from the Earliest Eocene of China, a new family Archicebidae has been erected, placed by the authors in their extended concept of Tarsiiformes (Ni et al. 2013). Whereas the placement of this fossil in early tarsiiforms or early omomyiforms or something else is debatable, its description adds considerably to our knowledge of the earliest primate radiation. It is represented by a crushed skull, isolated elements of the forelimb, and the entire rear part consisting of lumbar vertebrae, pelvis, tail, and both posterior limbs. Its skull length is approximately 2.5 cm, its long tail more than 13 cm, and its body weight is estimated to be 20–30 g. The crushed skull shows orbits of a relatively small size, indicative of likely diurnal habits. The skull shape is described as close to that of *Teilhardina asiatica*. The snout is said to be very short, as in *Tarsius* and some omomyids. The dentition is close to that of the other primitive primates; however, it shows a derived single-rooted P/2, and P1 and P2 appear reduced in comparison with adapiforms. The skeletal elements show elongated hindlimbs, long tibiae and long metatarsals, and other characters linked to a moderate leaping adaptation. Remarkably, the calcaneum of *A. achilles* is broad in its distal half, and is described as anthropoidean-like. Several of its tarsal characters are admitted as primitive in primates. The importance of this fossil lies, among other aspects, in the documentation of a calcaneum strongly different from that of *Teilhardina*–more primitive and associated with a moderate leaping adaptation – which substantially adds to our knowledge of early primate locomotor adaptations.

Eosimiidae

The Asiatic family Eosimiidae has provided crucial information and challenge concerning the early primate radiation (Beard et al. 1994, 1996). This family now includes three genera from the Middle Eocene of China and Thailand – *Eosimias* (three species), *Phenacopithecus* (two species), and *Bahinia* – and possibly a fourth one from the lower Oligocene of Pakistan – *Phileosimias*. The upper molars of *Eosimias* and *Phenacopithecus* are extremely primitive, transversely elongated with a marked waisting lingual to the labial cusps (Fig. 22); this waisting, very

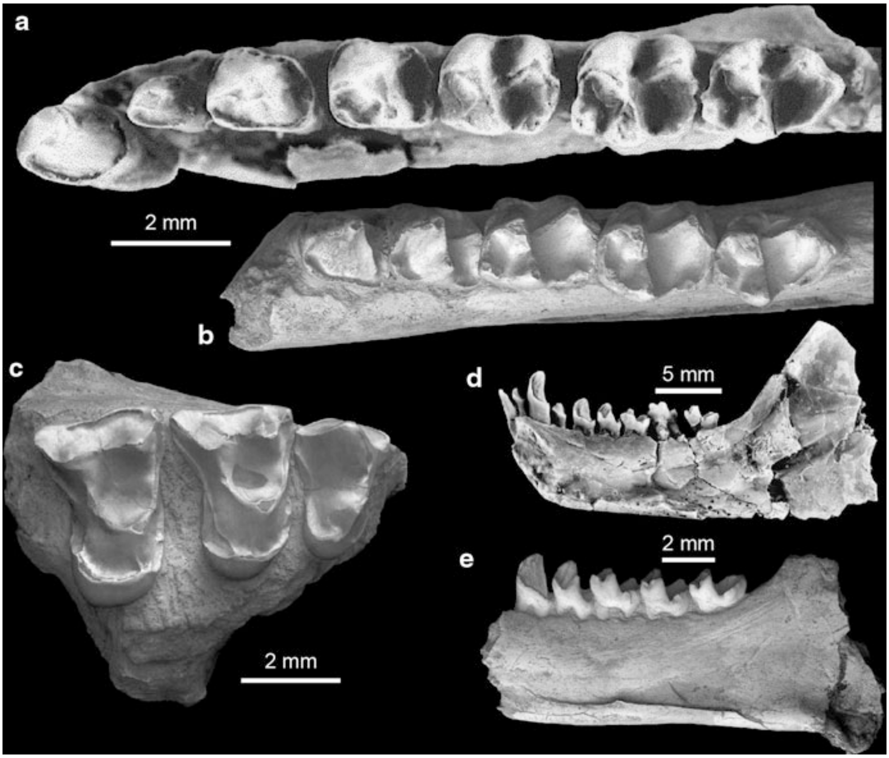

Fig. 22 Dentition of Eosimiidae. Mandibles of *Eosimias centennicus* in occlusal (**a** and **b**) and lingual (**d** and **e**) views. Maxilla of *Phenacopithecus krishtalkai* in occlusal view (**c**). Upper and lower molars are remarkably primitive, the two mandibles illustrate an interesting intraspecific dental variability, and premolars in (**e**) are reminiscent of *Xanthorhysis* (Courtesy of K. C. Beard)

marked on the posterior border of M1/, is also present on M2/, and is slightly marked on the anterior border of both teeth, which is exceptional (Beard and Wang 2004). On the labial side, there is a well-formed parastyle, as well as some labial extension of the crown labially to M2/, showing the remnant of a stylar shelf. These proportions give to these upper molars an extraordinarily primitive stamp. The complete lingual cingulum is derived in comparison with *Teilhardina* and *Donrussellia*; however, the absence of a hypocone by Middle Eocene time is very archaic in comparison with most other fossil primates. The upper P3/and P4/have narrow protocone lobes, presumably also primitive. The lower dentition as well shows many primitive characters. It is best documented on the two lower jaws of *Eosimias centennicus*, which show the complete lower dentition and aspects of the posterior part of the mandible (Beard et al. 1996). The incisors are small; I/2 shows one pointed cusp and I/1 was probably similar. Both incisors have a complete lingual cingulid. The canine is large, robust, and recurved anteriorly. A cingulid starts at the apex, descends posteriorly, and terminates as a posterior basal cingulid. There is a small, single-rooted P/2 bearing a single cusp and a posterior and lingual cingulid. P/3 and P/4, quite similar to each other, are massive, broad, and long premolars. P/3 is simple. Its massive protoconid has a curved preprotocristid in profile view and is surrounded by an almost complete cingulid. In occlusal view, its base shows an anterolabial bulge, associated with a labially shifted anterior root. P/4 is similarly massive and is more molarized, bearing a metaconid, a paraconid linked to the latter, and a more extended talonid. P/3 and P/4 have an almost complete labial cingulid, and on the labial side the enamel is ventrally extensive below the cingulid (exodaenodonty, easy to see on the anterior view of the isolated P/4 of *Phenacopithecus xueshii*; Beard and Wang 2004, Fig 16). Intraspecific variations in dental detail are described by Beard and Wang (2004). One of their specimens illustrates very well a degree of premolar crowding, by which P/3 is canted anterodorsally and its base is crowded below the anterior part of P/4, exactly as in the tarsiid *Xanthorhysis*. The main cusps of P/3 and P/4 are aligned with molar cusps as usual, but the bases of these cusps are anterolabially expanded, linked to a labial shift of their anterior root (Fig. 22). The three lower molars of *Eosimias* display a combination of high cusps recalling insectivorous species and rounded summits giving them a slight bunodont touch. They have a broad and elongated trigonid, bearing a big paraconid well separated from the metaconid. In occlusal view the trigonid is almost exactly the same from M/1 to M/3, a situation typical of tarsiids and exceptional in other Eocene prosimians. On the type specimen the notch on the protocristid is deeper (a deep V) on M/3 than on M/2. There is some waisting on the labial side of M/2 (ectoflexus) between the trigonid and the talonid. The talonid basin is deep, transversely broad, and anteroposteriorly short. A hypoconulid is posteriorly salient on M/2, being slightly closer to the hypoconid than to the entoconid. M/3 is noteworthy for the small size of its talonid, which is narrower than the trigonid, and for the small size of its third lobe, which is reduced to a very moderate hypoconulid (slightly less salient than in *Xanthorhysis*). The dentaries of *Eosimias* are relatively high and robust, with a vertical and anteroposteriorly short symphyseal region. The posterior part of the dentary of *E. centennicus* shows a rounded angular region and a small coronoid process.

Some important facial characters of eosimiids were revealed by a species of *Phenacopithecus*, another genus found in the Middle Eocene beds of the Heti Formation of Shanxi (Beard and Wang 2004). These species are close to *Eosimias*: they are larger and differ by some details of P/4 and other teeth. A maxilla of *P. krishtalkai* shows that this bone is high between the orbital margin and the alveolar rim. The orbits seem to have been small, suggesting diurnal activity. The infraorbital foramen is also relatively small; however, this is no more proof of haplorhinism.

Another eosimiid has been found in the late Middle Eocene Pondaung Formation of Myanmar, *Bahinia pondaungensis* (Jaeger et al. 1999). Two associated maxillae and a partial mandible revealed many dental characters of this species, which is larger than *Eosimias* and *Phenacopithecus*. The upper canine is especially large, with a rounded outline, and roots show that the upper incisors were vertically implanted, I1/being slightly larger than I2/. This morphology is said to resemble *Tarsius* more than the omomyids (Jaeger et al. 1999). The upper premolars have a

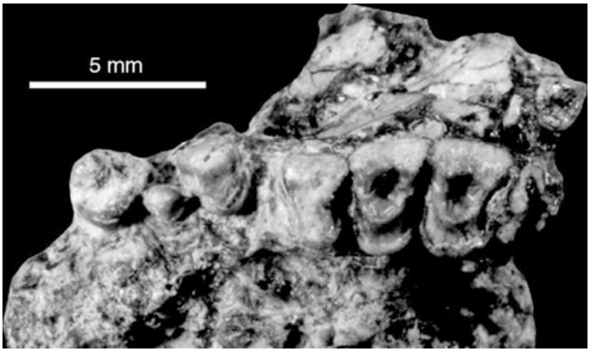

Fig. 23 Left part of the palate of *Bahinia pondaungensis* showing the broken canine, very small P2/, P3/, damaged P4/, M1/, and M2 (Courtesy of R. L. Ciochon)

lingual lobe but no differentiated protocone. The upper molars show well-developed protocristae, one joining the metacone, the crista obliqua, and another quite rare in primates joining almost directly the paracone (Fig. 23). These upper molars also have a thick labial and a continuous, strong lingual cingulum, with M2/ showing a slight thickening of the cingulum that represents an incipient hypocone. The P/2 is larger than in *Eosimias*. P/3 and P/4 are large, having roughly the same size. P/4 has no metaconid or paraconid, in contrast to *Eosimias*. The right maxilla allows the delineation of an orbit of small size, a relatively high distance between the ventral orbital rim (with exposed maxilla) and the alveolar margin, and a small zygomaticofacial foramen (Kay et al. 2004b).

Another eosimiid genus has been described from Early Oligocene beds of Pakistan (Marivaux et al. 2005). *Phileosimias kamali* is represented by eight isolated teeth (and the very close, possibly conspecific, *P. brahuiorum* by two upper molars). The upper molars differ from other eosimiids by well-formed conules, lingually rounded paracone and metacone (no crista obliqua), and a cuspidate hypocone on the M2/ of *P. brahuiorum*. The lower molars seem to have a more bunodont appearance and a somewhat reduced paraconid, slightly shifted lingually in comparison with *Eosimias*. The M/3 has a larger talonid with a broader third lobe than in *Eosimias*. The P/4 has a small crestiform metaconid and is narrow in its posterior part. P/3 and P/4 are slightly exodaenodont. If the affinities with more typical eosimiids are confirmed, this later taxon would illustrate a trend opposite to that seen in *Bahinia*: it increased bunodonty and the development of conules, whereas *Bahinia* increased its crests. Its smaller P/3 and P/4 also appear to represent a trend opposite to what is observed in *Eosimias*. The mention of an Early Eocene eosimiid *"Anthrasimias gujaratensis,"* in the Vastan Mine, India, is a misidentification (Bajpai et al. 2008; Rose et al. 2009).

Among the tarsals found in the Shanghuang fissure fills, one group is attributed to the eosimiids (Gebo et al. 2000, 2001). These tarsals present calcanea with whole proportions intermediate between those of the omomyids and tarsiids, which are narrower, and those of the anthropoideans, which are broader (see Fig. 35). They present a moderately elongated distal part (45–62 %), a long heel (28–36 %) and a relatively long and narrow posterior calcaneal facet. These characters suggest a mixture of quadrupedalism and leaping. Distally, these calcanea present a cuboid facet that is relatively flat, with a wedge removed from the medioplantar region. The astragali ascribed to eosimiids are moderately high, and also have a moderate neck angle. They possess a posterior trochlear shelf. Astragalar characters concur with those of the calcanea to suggest quadrupedalism, and more leaping than in platyrrhines (Gebo et al. 2001).

The phylogenetic affinities of Eosimiidae have been debated since their discovery. Many authors have followed Beard and collaborators, who defended close affinity with anthropoideans (an anthropoidean status with a stem-based definition of that group, or a stem anthropoidean or protoanthropoidean status based on our conventions), e.g., Kay et al. (1997), Marivaux et al. (2005), Williams et al. (2010). However, others have disagreed (Godinot 1994; Gunnell and Miller 2001; Simons 2003). The noteworthy aspects of the eosimiid dentition that need to be evaluated foremost are some of its extraordinarily primitive characters. Most authors agree that the transversely elongated upper molars, with the remnant of a stylar shelf labial to the metacone, marked waisting in the median part, and complete absence of a hypocone, are primitive characters – with the first two of these being more primitive than in *Teilhardina*, and thereby modifying the concept of the primitive primate dental morphotype. Such is also the case for the very large paraconid of the lower molars, especially on M/3. These observations raise further questions: Could the short M/3 talonid also be primitive in primates? Could the lower metaconid relative to the protoconid also be primitive by comparison with a primitive out-group, contrary to Gunnell and Miller (2001), who consider an equal height of these cusps likely to be primitive? These and other important questions will have to be scrutinized in the future. In any case, eosimiid dental features are leading researchers to modify the primitive primate dental morphotype, which plays a critical role in primate phylogenetic analyses.

Other characters that have been considered shared-derived with anthropoideans include P/3 and P/4 that are slightly exodaenodont and show an anterior root more labial than the posterior one. These features are shared with several early African simians; an oblique though not exodaenodont P/4 is considered part of the African simian morphotype by Gunnell and Miller (2001). Furthermore, these characters appear on P/3 and P/4 of very large size relative to the molars, larger than in any early African simian. Whereas the latter have a broad and short P/4 and a relatively large P/2, *Eosimias* has long, anterobasally inflated P/3–4 reflecting a peculiar adaptation emphasizing these big premolars, associated with a reduction of its P/2. This suggests the possibility of a partial functional convergence leading to labial reinforcement and some exodaenodonty of P/3–4 (probably also to a high and robust dentary). The vertically implanted lower incisors and the short vertical symphyseal region are shared with anthropoideans, but they can also be expected in haplorhines having acquired an abbreviated snout. As these incisors are very small and pointed, whereas those of anthropoideans are spatulate and usually larger, there is little evidence of characters exclusively shared with anthropoideans; these observations more probably indicate a haplorhine grade. It is difficult to find convincing phylogenetic signals in the very primitive molars of *Eosimias*. There is some convergence between more crested genera, as e.g., in the eosimiid *Bahinia* and the anthropoidean *Catopithecus*, which acquired a complete crista obliqua and an almost continuous crest linking protocone and paracone. However, known lower teeth of *Bahinia* are very different from those of oligopithecids, making a close link between them unlikely. The bunodont trend in eosimiids possibly led to the Oligocene *Phileosimias*, which is far from any known African simian. In the absence of indisputably derived characters homologous with those of African simians, are there other possible phylogenetic links? A sister group relationship with Amphipithecidae was advocated by Jaeger et al. (1999), and thus is examined below with that group.

A probable close affinity between *Eosimias* and the tarsiid *Xanthorhysis* has been mentioned above. The lower molars are higher and more pointed in *Xanthorhysis*. The P/3 and P/4 share a similar global pattern, including even the peculiar crowding between P/3 and P/4 described above. *Eosimias* appears as a more bunodont version of *Xanthorhysis*, having increased the size of its P/3 and the anterobasal robustness of its P/3–4. Found in omomyids, such differences would not prevent the placement of two genera in the same subfamily, because the overall pattern is so similar. This is significant and should not be ignored. The resemblance is not a proof of direct tarsiid affinities, however, because *Xanthorhysis* might turn out to be the most primitive eosimiid. Not enough is known about *Tarsius eocaenus* and its possible close relatives to decide on this. However, the similarity clearly does point towards close affinities between the two families. In this context, the recently introduced concept of Eosimiiformes appears problematic (Chaimanee et al. 2012).

Certain facial characters mentioned above show that the eosimiids were probably diurnal. Being diurnal is sometimes considered a challenge for possible tarsiiform affinities (Beard and Wang 2004); however, as seen above, early haplorhines are in fact expected to be diurnal (Cartmill 1980; Ross 1996). Thus Tarsiiformes other than tarsiids or tarsiines are expected to be diurnal, as eosimiids are. The simplest scenario, backed up by the strong dental similarities between *Tarsius, Xanthorhysis*, and *Eosimias*, is that eosimiids are tarsiiforms, and are character-based haplorhines. An isolated petrosal from the Shanghuang fissure fillings, attributed to an eosimiid, may add to our knowledge of eosimiid cranial anatomy (MacPhee et al. 1995). This petrosal exhibits a large canal reflecting a fully functional stapedial artery. Large and subequal stapedial and promontorial canals are also found in *Shoshonius* and *Omomys*; they contrast with another omomyid (*Necrolemur*) and *Rooneyia*, in which the stapedial canal is consistently smaller, and even more with the anthropoideans and *Tarsius*, in which it is further reduced or lost (probably convergently). The authors conclude that for this character, eosimiids probably retained a primitive state. They also conclude that eosimiids preceded the reorganization of the anthropoidean ear region (MacPhee et al. 1995), which agrees with a tarsiiform or an omomyiform view. The postcranial evidence for eosimiids has also been used to argue in favor of anthropoidean affinities. However, there are a number of caveats to be noted. Thus, a wedge in the plantar region of the cuboid facet developed in several primate groups. Astragali of eosimiids have a posterior trochlear shelf, which is absent in anthropoideans.

They share with anthropoideans a reduced medial tibial facet, but this character is likely primitive in primates. In other respects they are, in the words of Gebo et al. (2001, p. 96) “unlike anthropoids and resemble omomyids.” Postcranial characters are further discussed below in the anthropoidean origins part. The extreme leaping specialization of the living *Tarsius* leads one to suspect that primitive tarsiids were less specialized, as seen in the Shanghuang tarsiids; *a fortiori*, other early tarsiiforms are expected to be differently adapted, more quadrupedal. In conclusion, eosimiids probably fit in among early tarsiiforms (unless the petrosal, if well attributed, indicates omomyiforms).

North American and Asiatic Enigmas: Rooneyiidae, *Ekgmowechashala*, and Amphipithecidae

Rooneyiidae

The two North American genera *Rooneyia* and *Ekgmowechashala* occurred relatively late, in the Latest Eocene and in the Oligo-Miocene, respectively. They were both included in the systematic revision of the Omomyidae by Szalay (1976) and continue to be considered a possible tribe of omomyines, in the case of *Rooneyia*, and a problematic omomyid, in the case of *Ekgmowechashala* (Gunnell and Rose 2002). However, their status is questioned in several recent analyses. *Rooneyia viejaensis* is known by its type cranium from the Late Eocene of Texas, which is well preserved (Wilson 1966). Its upper dentition is bunodont and anteriorly abbreviated. The upper molars bear large conules (and P4/ a large paraconule) and a hypocone almost as large as the protocone on M1/. There are only two upper premolars and a very small canine. The bunodont molars bear similarities with those of anthropoideans, whereas the two premolars resemble only those of catarrhines. However, the small canine together with other cranial characters exclude a close affinity with the latter. Nevertheless the cranium of *Rooneyia* shows a number of characters which make this genus unique among primates. It shares with omomyids the presence of a tubular ectotympanic. Differences with omomyids include the lack of any inflation of the petromastoid region and relatively small orbits which suggest diurnal habits, contrary to other omomyids (with the exception of *Teilhardina*). Characters unique to *Rooneyia* concern its orbits. The large frontal with fused metopic suture extends above the orbit as a partial roof; the lateral frontal process is high and constitutes an incipient postorbital closure; the orbital fossa is funnel-shaped and pushed slightly below the forebrain (Rosenberger 2006). In addition, the orbits of *Rooneyia* show high degrees of convergence and frontation which position this taxon closer to living anthropoideans than to living prosimians (Ross 1995). These characters led Rosenberger (2006) to propose for *Rooneyia* a formal status of Protoanthropoidea. The unique combination of characters found in *Rooneyia* resulted in various placements. The large cladistic analysis of Kay et al. (2004b) led to a preferred tree in which *Rooneyia* appears nested within the adapiform radiation, as a primitive sister group of a clade (amphipithecids +

Fig. 24 Lower dentition of *Ekgmowechashala philotau*. Supplementary cusps are present on P/4 and molars, and the very low relief can be seen on M/3, which is less worn than the other teeth. Photograph of a white-coated epoxy cast

adapids). However, in the phylogenetic analysis of Ni et al. (2010), *Rooneyia* appears nested within the washakiins, which seems hard to reconcile with the cranial characters of *Shoshonius*. In view of these contradictory results, it seems important to acknowledge the uniqueness of *Rooneyia* by using a family Rooneyiidae, and to keep in mind its important protoanthropoidean-like orbital characters. Because it is known that faunal exchanges between North America and Asia occurred repeatedly, it would be fruitful to pursue comparisons of *Rooneyia* with bunodont Asiatic primates.

Ekgmowechashala

Ekgmowechashala philotau occurs in the Late Oligocene to Early Miocene of South Dakota and Oregon, more than 10 My later than *Rooneyia*. It is known by a dentary with P/3–M/3 and upper P4/–M1/ and half of M2/. The dentary is elongated. Upper and lower P4 and molars have a low relief, heavily crenulated enamel, and supplementary cuspules (Fig. 24). The upper molars have large conules and a large hypocone shifted anteriorly, which is linked to the protocone and sometimes interpreted as arising from a protocone fold. The lower molars have a large cuspidate metastylid and a low posteriorly opened trigonid without paraconid. Both upper and lower P4 have large anterior cusps and a posterior basin. P/2 and P/3 are simple. Alveoli suggest the presence of two small incisors and a larger canine. P/2 is double-rooted, which is otherwise unknown in any omomyid. These dental details have often been compared with those of *Rooneyia*, and *Ekgmowechashala* was at one point thought to be derivable from a form close to *Rooneyia* (Rose and Rensberger 1983). However, the two roots of the P/2 are problematic, suggesting primitively little reduced premolars, contrary to what is seen in the uppers of *Rooneyia*. The two-rooted P/2 is probably among the characters which led to a placement close to *Adapis* in the phylogenetic analysis of Ni et al. (2010). On the whole, the phylogenetic place of *Ekgmowechashala* appears unresolved. Is it possible that there was an unusual, atavistic reversal from one to two roots in P/2? A putative rooting close to the highly bunodont *Chipetaia* might be further explored, as well as possible Asiatic clues.

Amphipithecidae

The Amphipithecidae are a group of Asiatic species found mainly in late Middle Eocene beds of Myanmar; one species comes from the Late Eocene of Thailand, and a small genus possibly survived in the Oligocene of Pakistan. Since the discovery of the fragmentary jaws of *Pondaungia cotteri* (Pilgrim 1927) and *Amphipithecus mogaungensis* (Colbert 1937), the overall similarity of this group with the anthropoideans has been recognized. However, they also show peculiar characters which prevent their placement within the African simian radiation, possibly suggesting affinities with a prosimian group (Szalay and Delson 1979). Associated postcranials have increased the controversy. Despite a growing fossil record, no cranial specimen is complete enough to prove the anthropoidean status of amphipithecids.

The Pondaung Formation of central Myanmar yielded a series of specimens of *Pondaungia* and *Amphipithecus*, the two best documented genera, as well as rare specimens of two other species, *Myanmarpithecus yarshensis* (Takai et al. 2001) and *Ganlea megacanina* (Beard et al. 2009). Species of *Pondaungia* and *Amphipithecus* are close in morphology, showing short, high, and heavy jaws with vertical symphyseal region, parabolic tooth rows in occulsal view, and very bunodont teeth. Importantly, their symphyses are not fused. Many specimens show heavily worn teeth. There are two different sizes in specimens of *Pondaungia* from Pangan and Mogaung, suggesting either a high sexual dimorphism or the presence of two species. Due to the larger-sized specimens being more abundant, Takai and Shigehara (2004) consider the assumption of two species more parsimonious, in which case the large one should be called *P. savagei* (Gunnell et al. 2002). Details of dental morphology seen on *Amphipithecus mogaungensis* include short, wide, posterolingually extended P/3 and P/4 (Fig. 25). These teeth have no well-formed metaconid, only irregularities (cuspules?) on a postero-lingual crest descending from the protoconid summit. A small hypoconid is present on the summit of the posterior cingulid. Its lingual crest joins the preceding crest, or the lingual cingulid on P/3, to surround a talonid basin reduced to a narrow and inclined gully. The lower molars have a long, broad, and shallow talonid basin. Their outlines show a median waisting. The cusps of trigonid and talonid have the same height; they are rounded, robust, low, and highly bunodont. The trigonid is antero-posteriorly short, longer on M/1. There is no hypoconulid. The enamel is smooth on most molars of *Amphipithecus*, which has a small M/3. *Pondaungia* has crenulated enamel and a large M/3. The jaws of the large *Pondaungia* are especially high and longitudinally curved (Jeager et al. 1998), whereas jaws of the smaller *Amphipithecus* are less extreme. Unworn molars of *Pondaungia* show interesting details, among them M/1 having a paraconid, a continuous anterior paracristid joining the metaconid, a

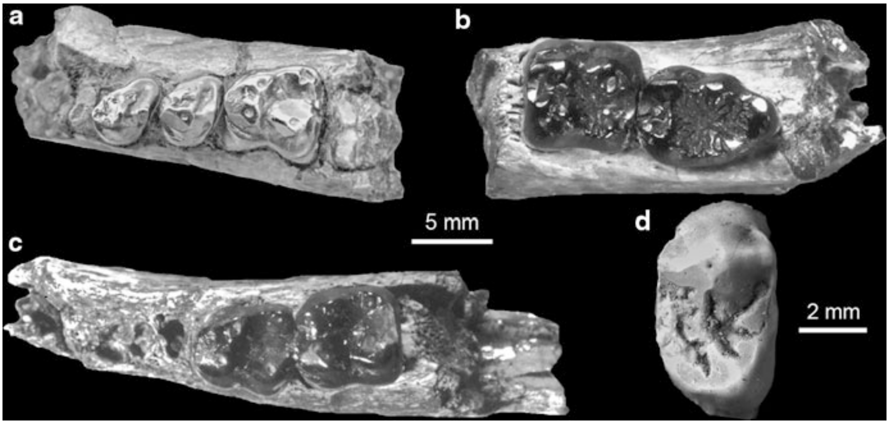

Fig. 25 Dentition of *Amphipithecus* and *Pondaungia*. Left mandibles of *A. mogaungensis* showing P/3, P/4, and M/1 (**a**) and M/1 and M/2 (**c**). Mandible of *P. savagei* showing unworn M/2 and M/3 (**b**) and P4/ of *Pondaungia*, possibly *P. cotteri* (**d**). All are in occlusal views (Courtesy of R. L. Ciochon)

bicuspid metaconid, and a small hypoconulid arising from the postcingulum as in many primitive primate groups.

The upper teeth are correctly documented since the discovery of a maxilla and associated I1/ and canine of *Pondaungia* (Shigehara et al. 2002), and other specimens including a complete unworn P4/ (Gunnell et al. 2002). The I1/ is large, robust, and spatulate. The canine is very large and oval in cross-section. It bears a lingual cingulum and a shallow vertical ridge on its lingual side. P3/ is transversely elongated with rounded extremities and has a protocone only slightly narrower than the paracone. A beautiful P4/ is more transversely elongated than P3/, and shows an anteriorly located protocone issuing three crests (pre-, postprotocrista, postprotocingulum) and a large paraconule. Both protocone and paracone are massive and inflated, yet there is no labial or lingual cingulum as in bunodont simians (Fig. 25). The upper molars are rectangular in outline, with some narrowing of the posterior half of the M2/ in both *Amphipithecus* and *Pondaungia*, and some narrowing of the lingual part of the M1/ in *Amphipithecus* only (Takai and Shigehara 2004). The upper molars are better preserved on specimens of *Pondaungia*, in which they are particularly low-crowned and crenulated. The four major cusps have a rectangular disposition, the hypocone clearly having a strong link to the protocone. Due to this position, isolated from a lingual cingulum on M2/, the hypocone has been interpreted by some authors as a pseudohypocone issued from the posterior flank of the protocone, which would be a rare similarity shared with notharctine adapiforms. However, it is difficult to distinguish those aspects of dental traits which are due to an extreme bunodont adaptation and those which reflect ancestral features of the group. A strong link between hypocone and protocone can develop on a cingular hypocone, e.g., in *Necrolemur*. A pseudohypocone homologous with notharctines is unlikely (Shigehara et al. 2002),

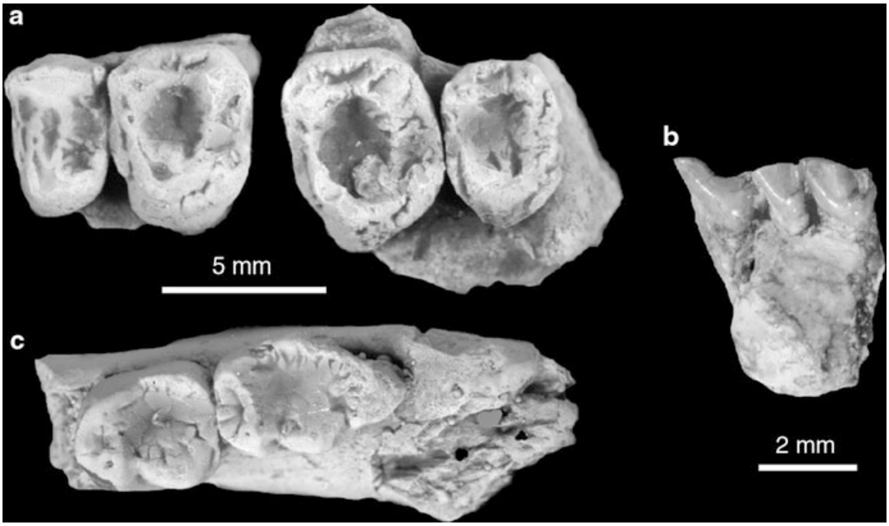

Fig. 26 Dentition of *Myanmarpithecus yarshensis*. Upper teeth P4/ to M3/ (**a**) and lower molars M/2 and M/3 (**c**) at the same scale. The fragment of anterior jaw with canine, P/2, and P/3 in lingual view (**b**) is at a different scale (Courtesy of R. L. Ciochon)

and interpretation of this cusp as a displaced metaconule as in artiodactyls (Coster et al. 2013) is also unlikely. The less derived morphology of *Myanmarpithecus* and *Ganlea* leads to the suspicion that the hypocone of amphipithecids is a cingular one, as in most primates.

Maxillae are known from both *Amphipithecus* and *Pondaungia*. In dorsal view both show an unusual groove on the lateral side of the orbital floor, just medial to the zygomatic wall (Shigehara and Takai 2004). The orbital floor is very flat in *Amphipithecus*. Its posterior border does not show any posterior protrusion as seen in taxa with postorbital closure, indicating that this taxon had an incomplete postorbital closure at the most. However, there is no evidence against or in favor of any development of a posterior part of postorbital closure (Shigehara and Takai 2004). In lateral view, the distance between the base of the orbit and the alveolar rim is moderate: higher than in lemuriforms (nocturnal, with large orbits) but lower than in anthropoideans of comparable size (Shigehara et al. 2002). From the relative size of the upper premolars and the shape of the zygomatic root, Shigehara and Takai (2004) deduce that *Pondaungia* was probably a diurnal primate with a relatively short muzzle. An isolated bone found in close proximity with a maxilla of *Amphipithecus* was initially interpreted as a frontal of this taxon (Gunnell et al. 2002; Takai and Shigehara 2004). It figured in discussions until it was shown to be misidentified, and certainly not to be a primate frontal (Beard et al. 2005).

Myanmarpithecus yarshensis is a small species that also presents highly bunodont teeth and crenulated enamel (Takai et al. 2001). Its upper teeth have more rounded lingual outlines than in the above-mentioned species (Fig. 26).

Despite the fact that the specimen is worn and some details are invisible, the small hypocone on M1/ and M2/ is seen to be peripheral and seems placed on a broad posterolingual cingulum. It would thus seem to be a cingular hypocone. The P4/ is somewhat transversely elongated and has an anteriorly placed protocone without lingual cingulum. A partial left mandible shows C, P/2, and P/3 all with posterolingual expansion and cingulid, bearing resemblance to platyrrhine teeth. This expansion on P/3 is also reminiscent of *Amphipithecus*, even if the tooth is more elongated. M/2 and M/3 have anteroposteriorly compressed trigonids, with an apparently complete paralophid joining the summit of the metaconid. Low relief and reduced labial cingulid are as in other amphipithecids; the M/3 third lobe is elongated. The compressed trigonid and extended M/3 lobe are reminiscent of some fossil prosimians, but no close tie to any one of them has been suggested.

The most recently described amphipithecid *Ganlea megacanina* (Beard et al. 2009) adds interesting information. In size and several aspects of its morphology, it appears intermediate between *Myanmarpithecus* and *Pondaungia*, confirming the place of the former. It also has an enormous canine showing very strong apical wear. P/3 and P/4 are less anteroposteriorly compressed than in *Pondaungia*. P/4 has a relatively large metaconid, P/3 has none. Both premolars have an anteriorly elongated preprotocristid with a paraconid, especially high on P/3, resulting in a very unusual profile for this tooth. An unworn upper molar, interpreted as M1/ or M2/, has a rounded outline as in *Myanmarpithecus*, crenulated enamel, no conules, and only a small cuspule on the posterior cingulum that might be an incipient hypocone. Like other amphipithecids, *Ganlea* was probably a hard-object feeder (Shigehara et al. 2002; Kay et al. 2004a; Beard et al. 2009). The apical wear of its large canine is similar to what is seen in living pitheciines, which are specialized on hard fruits. The same kind of apical wear on canine and premolars is present on *Myanmarpihecus*, which is smaller than living pitheciines.

The large *Siamopithecus* from the Krabi mine in Thailand (Late Eocene) is probably the most extreme in its bunodonty (Chaimanee et al. 1997; Ducrocq 1999). Its upper molars are particularly extended transversely. Their hypocone bears unusual links, being anteriorly directly linked to the protocone, posterolingually directly to the posterior cingulum, and, in the case of M2/, also directly linked to the metacone by a lingual crest. The absence of the crista obliqua linking protocone and metacone, replaced on M2/ by a crest linking hypocone and metacone, as in *Pondaungia*, stands in stark contrast with the morphology of most anthropoideans. The massive, anteroposteriorly long and transversely short P3/ and P4/ are also very distinctive – much more reminiscent of a giant omomyiform than of an anthropoid. To what degree are these premolars autapomorphic, obscuring phylogenetic signals? Maxillary and facial fragments associated with a lower jaw of Krabi have been used to produce a reconstruction of facial elements through synchrotron microtomography, followed by adjustment of digital images (Zollikofer et al. 2009). Despite the fragmentary nature of the remains, the positioning of two parts of the orbital rim suggests that *Siamopithecus* had highly convergent and frontated orbits, as is typical of living anthropoideans. Convergence does not seem so high from the figures, whereas frontation does; it looks higher than in the African simian *Parapithecus*. Estimations of these parameters as well as a morphometric study based on landmarks place *Siamopithecus* phenetically within anthropoideans. However, this fossil is still fragmentary and does not show the key characters of postorbital septum or middle ear morphology that would definitively prove an anthropoidean status.

A small species from the Oligocene of Pakistan, *Bugtipithecus inexpectans*, is represented by six isolated teeth having unusual characters (Marivaux et al. 2005). It is less bunodont than the genera discussed above; it shows a well-formed small cingular hypocone with a prehypocrista linking it to the postprotocrista, a cuspidate metaconule, and labial and lingual cingula on the upper molars. This small survivor may well illustrate primitive character states for amphipithecids. These would point toward a possible connection with eosimiids (posterior waisting, parastyle, salient hypoparacrista on M1/, morphology of P/4), but not with primitive African simians.

The controversies about amphipithecid affinities have been fueled by the discovery of a small set of postcranial specimens, probably of the same individual, in the Pondaung Formation. These bones ("NMMP 20") have the right size to be attributed to species of *Pondaungia*, but have a series of characters that are difficult to reconcile with anthropoidean affinities (Ciochon et al. 2001). An almost complete humerus shows a reduced deltopectoral crest, a shallow bicipital groove, a rounded capitulum with an expanded capitular tail, a groove separating the capitulum and the trochlea and a lateral trochlear rim, an expanded lateral epicondyle, and the absence of a dorsoepitrochlear pit (Fig. 27). On the one hand, these characters and others constitute important differences from anthropoidean humeri, while on the other they present similarities with notharctine adapiforms. However, there are also differences from known notharctines, e.g., a distomedially sloping trochlea, a proximally salient humeral head, and a few other traits. There are also a proximal ulna, a calcaneum lacking its proximal tuber, and other fragments. The calcaneum is quite different from that of simians, showing similarities with notharctines or adapines, as well as a few differences (Fig. 27). The calcaneocuboid facet has similarities with that of *Adapis* in its marked dorsoventral orientation (Ciochon and Gunnell 2004). Functionally, many characters reflect mobile joints and stability, as in slow-mowing arboreal quadrupeds (Kay et al. 2004a). In terms of affinities, most authors agree that these characters are at odds with anthropoidean affinities, leading to two different propositions: (i) they confirm a notharctid origin for amphipithecines (Ciochon et al. 2001; Ciochon and Gunnell 2004); (ii) they must not pertain to *Pondaungia*, considered an anthropoidean, but to a yet unsampled large sivaladapid adapiform, because small adapiforms were found in the Pondaung Formation and large sivaladapids did exist in Asia (Beard et al. 2007). A partial pelvis, found at the same locus and probably pertaining to the same individual, shows strepsirhine rather than anthropoidean affinities, according to Marivaux et al. (2008).

Two isolated astragali from the Pondaung Formation have been successively described, both of which have the right size to be attributed to a large-bodied amphipithecid (Marivaux et al. 2003, 2010). They show no adapiform/strepsirhine character but similarities with omomyids and simians, and have been interpreted in

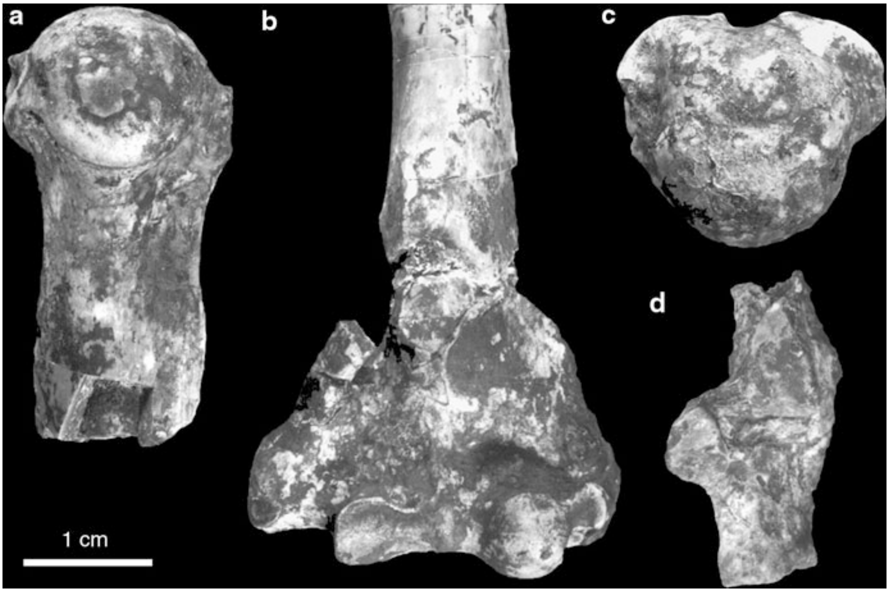

Fig. 27 Some elements pertaining to the controversial NMMP 20 set of postcranials possibly pertaining to *Pondaungia savagei*. Proximal left humerus in posterior (**a**) and proximal (**c**) views; distal left humerus in anterior view (**b**); and distal calcaneum in dorsal view (**d**). All at the same scale (Courtesy of R. L. Ciochon)

favor of simian affinities for amphipithecids (Marivaux et al. 2003, 2010; Dagosto et al. 2010). These bones are clearly lacking the derived strepsirhine/adapiform astragalar characters. However, their similarities with anthropoideans are not definitive proof of simian affinity because, as will be explained below, many of these characters are essentially primitive in primates, allowing only a "haplorhine" (sensu non-strepsirhine) identification (Dagosto et al. 2010).

The postcranial evidence for large-bodied primates from the Pondaung Formation is embarrassing. When the bones are possibly anthropoidean-like, they are attributed to amphipithecids. If they are clearly non-anthropoidean in their characters, proponents of the anthropoidean status of amphipithecids ascribe them to a yet unsampled large sivaladapid. However, it is strange that the growing number of fossil finds in the Pondaung Formation has not to date included discovery of such a large sivaladapid, whereas the number of large amphipithecid specimens has increased considerably. The alternative possibility is that the NMMP 20 bones and the astragali pertain to amphipithecids, and that this group is neither adapiform nor anthropoidean, but instead constitutes some kind of large "haplorhine" primate.

On the whole, craniodental remains of amphipithecids show tantalizing similarities with anthropoideans in the height and robustness of the mandibles, vertical symphysis, and many aspects of the bunodont dentition. But at the same time there are many differences with African simians which prevent researchers from positing a close affinity with propliopithecids or parapithecids (e.g., the latter have big conules and a large hypocone that is never linked to the metacone on the upper molars, short upper premolars with continuous lingual cingulum, lower molars with big hypoconulids, short M/3 lobe, etc.). Some characters of amphipithecids, such as the unfused symphysis in large bunodont species and the waisted lower molars, even more strongly suggest convergent evolution with African simians in other bunodont features. If they were anthropoideans, they would be very distantly related to African families, contrary to the results of numerous recent cladistic analyses. The weakness of parsimony analyses including large dental data sets, applied to very distantly related groups and a fossil record full of gaps, is stunningly apparent in the analysis of Kay et al. (2004b), in which Amphipithecidae are jumping from a place within crown anthropoideans to a place within fossil adapiforms, as a result of a slight change in analytic procedure. The program is evidently trying to ally them with the group presenting the highest number of shared derived characters. However, in an analysis including such primitive taxa as *Teilhardina* and *Donrussellia*, almost all characters of amphipithecids are derived relative to these primitive genera. In the absence of truly diagnostic characters, a high number of similar derived characters of the dentition and the postcranials can show up in two very different groups. What such analyses produce is more a signal of global phenetic similarity than a signal of phylogenetic affinity. The two extremely different results reveal that there is no clear phylogenetic signal in this analysis. Clearly, the data at hand do not allow elucidation of the problem. A similar analysis performed by Beard et al. (2009) nested amphipithecids within African simians; however, we know that this phylogeny is incorrect because *Amphipithecus* and *Pondaungia* lack complete postorbital closure. This demonstrates that a considerable amount of convergence in dental characters occurred, as indicated by the dental characters themselves. In spite of the appealing anthropoidean-like reconstruction of *Siamopithecus* facial parts, *Amphipithecus* and *Pondaungia* lack one of the diagnostic anthropoidean characters; furthermore, their suborbital region is lower than in anthropoideans of similar size (Shigehara et al. 2002), confirming convergence in cranial characters among haplorhine groups. Amphipithecids appear as highly bunodont diurnal primates, convergent with some simians in their craniodental specialization for hard-object feeding.

A sister group relationship between amphipithecids and eosimiids has been suggested by Jaeger et al. (1999). The probability of such a connection has since been increased by the discovery of *Myanmarpithecus*, which partly bridges the gap. It has been strengthened further by the discovery of *Bugtipithecus* and *Phileosimias*. The phylogenetic analysis of Marivaux et al. (2005) showed the two groups to be close, although their analysis continued to ally amphipithecids with African anthropoideans. Such a connection suggests the possibility that amphipithecids are derived from eosimiids and should be placed along with them in Tarsiiformes. As seen above, such a placement fits with the facial and postcranial characters. The two families would considerably broaden the adaptive spectrum of tarsiiforms, and in doing so reset the balance between the two major clades of haplorhines, simiiforms and tarsiiforms.

African Paleogene Anthropoidea or Simiiformes

A whole radiation of anthropoideans, or simians, is documented from the Late Eocene and Oligocene of Egypt. Extensive exposures in the Fayum desert have been yielding fossil primates since the beginning of the twentieth century. Renewed efforts of field crews led by Elwyn Simons and the Egyptian Geological Survey since the 1960s have resulted in the establishment of a succession of faunas, situated in a precise stratigraphic sequence (e.g., Simons 1995). Comparisons with similar faunas from Oman, which are linked with marine deposits, and magnetostratigraphy have led to a new dating of the section (Seiffert 2006). The most productive beds are those of the Jebel Qatrani Formation, which is mostly Oligocene: only one third of the "lower sequence" is Late Eocene in the new temporal framework. The older fauna called BQ-2, found in the Birket Qarun Formation and dated around 37 Ma, has yielded the oldest known undoubted anthropoids (Seiffert et al. 2005b). All families have at least one genus known by its skull. These fossils can thus be included in character-based anthropoideans; they possess their hallmarks, that is, a simian type of postorbital closure and the typical ear region (detailed below for *Parapithecus*).

Parapithecidae

The family Parapithecidae contains a group of four tightly united genera, *Apidium, Parapithecus, Qatrania*, and *Abuqatrania*, which can be considered as Parapithecinae, and the more primitive genus *Biretia*. The oldest and smallest species, *Biretia fayumensis* from BQ-2, shows relatively bunodont upper molars with a large cingular hypocone, a distinct paraconule on M1/, and well developed metaconules on M1–2/, P3/ and P4/ which have small hypocones and a P2/ transversely elongated, with a protocone and three roots (Seiffert et al. 2005b). These characters are shared with some later parapithecines. The lower molars show a moderate bunodonty and a centrally placed hypoconulid. They also retain a complete protocristid and a premetacristid, which will be lost in the later, more extreme bunodont species. P/4 has a cuspidate metaconid linked to the anterolingual cingulid, a hypoconid, and lingual talonid basin; its outline is somewhat anteroposteriorly elongated, whereas it becomes shorter and broader in several later species. It is a small species, with molars between 2 and 3 mm in length and a weight estimate of roughly 200 g. The slightly larger *B. megalopsis*, from the same locality, differs in a few dental details. Its maxilla reveals surprising features: the suborbital region is very shallow, resulting in the exposure of the roots of M1/ and M2/ in the orbital floor, which is formed at their level by the same bony lamina as the palate. The authors infer large orbits and a nocturnal adaptation for *Biretia*, whereas all later African anthropoideans are diurnal (Seiffert et al. 2005b).

Species of *Qatrania* and *Abuqatrania* are also small (length of P/4–M/3 less than 1 cm). Their lower molars are extremely bunodont and somewhat high-crowned (Fig. 28). Their crests are reduced, and their cusps are low and rounded, expanded

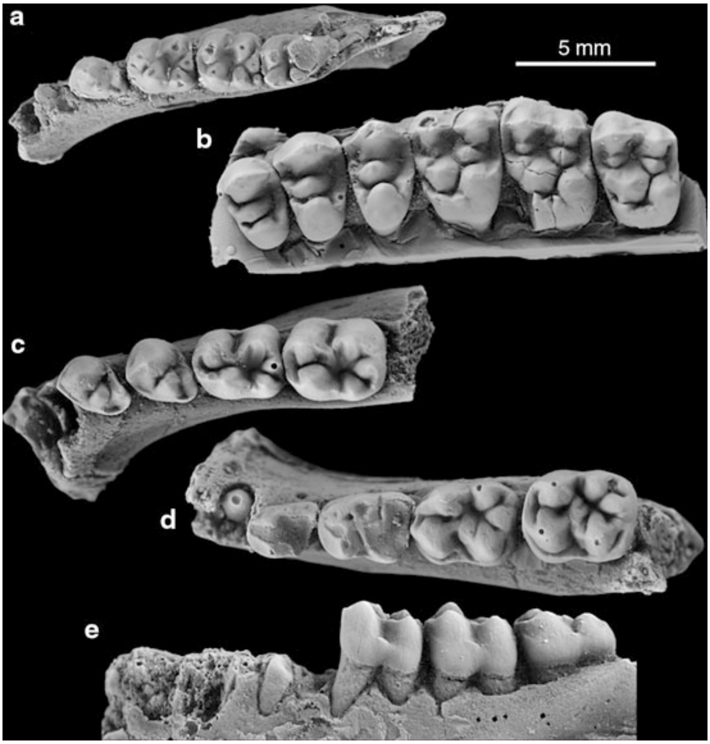

Fig. 28 Dentition of parapithecids. Right lower mandible of *Qatrania wingi* (**a**); maxilla (**b**) and mandibles (**c** and **e**) of *Parapithecus*, probably *P. grangeri*; and left mandible of a juvenile *Apidium phiomense* with worn milk teeth DP/3 and DP/4, and definitive M/1 and M/2 (**d**). The high degree of bunodonty is striking, and the maxilla also shows the supplementary cusp present on the three premolars and the great size of the hypocone, larger than the protocone on M1/ (**b**). All in occlusal views except (**e**), which is a labial view with M/1-M/3. Photographs of white-coated epoxy casts, all at the same scale

into the talonid basins. There is a large centrally placed hypoconulid. M/1 bears a small paraconid. On M/2 and M/3, protoconid and metaconid are separated by an anteroposterior groove; the protocristid is lost. The P/4 is short and simple, with a small metaconid and hypoconid. The mandibular rami of these species have been reported as very shallow (Simons and Kay 1988), and this is beautifully illustrated by the mandible of *Abuqatrania basiodontos*, which has both a very shallow ramus and a high and anteroposteriorly short coronoid process (Simons et al. 2001). One upper molar of *Qatrania* has a very large hypocone. Species of these genera differ by small dental details. The absence of a small posterolingual shelf (fovea) on the M/2 of *A. basiodontos* is emphasized as different from species of *Qatrania*. However, this is a primitive character state, found in the oldest species (from L-41). Placing that species in a different genus may obscure its likely ancestral status relative to the later species, *Q. wingi* and *Q. fleaglei*, from Oligocene levels.

Apidium and *Parapithecus* are clearly larger species found in the Oligocene beds. They are much better known and allow the description of skull and postcranials of parapithecids. There are two species of *Parapithecus*: the type species *P. fraasi*, known through its type mandible described by Schlosser (1911), from an unknown level, and *P. grangeri* (sometimes *"Simonsius" grangeri*), known by more material from Oligocene quarries and now including a cranium (Simons 2001). The lower molars and premolars are larger and accentuate the bunodont characters of *Qatrania*, showing, e.g., a longer and deeper groove between protoconid and metaconid on the lower molars, a larger metaconid isolated from the protoconid by a groove, an anterolingual cingulid and an abbreviated talonid on P/4. P/3 is similar to P/4 on *P. fraasi*, and P/2 is simpler, unicuspid, and bordered by a continuous lingual cingulid. The canine is moderate in size and shows an anterolingually ascending cingulid. The two species differ in size, in some dental details, and in the retention in the type mandible of *P. fraasi* of one incisor on each side, which is of light color and suspected to be a retained deciduous incisor, whereas *P. grangeri* has no more lower incisors at all – a morphology exceptional among simiiforms. The upper teeth are also extremely bunodont. On M1/ and M2/, the rounded cusps are inflated and the conules large, reducing the trigon basin (Fig. 28). The hypocone is almost as large as the protocone on M1/, smaller on M2/ (Kay and Williams 1994). P3/ and P4/ have a paraconule and P2/ appears transversely shorter on the cranium (Simons 2001). The alveoli reveal that there was a moderately large upper canine and two small incisors. Two anterior lower canines appressed against each other with intersticial wear, and wearing flat apically against the upper incisors, constitute a unique dental device – one that is strange in a species reported to be dentally dimorphic. The highly bunodont molars of parapithecids are interpreted as broadly adapted to frugivory, with nuances; e.g., a higher shearing capacity in *Parapithecus* may reflect a slightly more folivorous diet (Kay and Simons 1980).

The cranium of *P. grangeri* is fascinating. It has the complete postorbital closure typical of simians and at the same time an elongated profile recalling more primitive primates (Simons 2001, 2004). Its orbits are posterolaterally inclined in dorsal view, giving a convergence angle of about 105°, and posterodorsally inclined in lateral view, showing a frontation lower than in other simians, similar to some prosimians (Fig. 29). Among its noticeable characters are a large zygomatico-facial (or malar) foramen, as found in some platyrrhines; a glenoid fossa shaped as a transverse trough; a transversely extended postglenoid process; a lateral pterygoid wing extending posteriorly to overlap the lateral bullar wall; a relatively anteriorly located foramen magnum; and a relatively small braincase revealing an encephalization much lower than in living anthropoideans, comparable to that of Eocene prosimians (Simons 2001). This latter assessment depends on body size estimates; those based on dental regressions had initially given body weights ranging from 1.6 to 3 kg. More reliable estimates based on postcranials showed that 1.6 kg is the more likely value (Simons 2004). Even with this low estimate, a better calculation using a CT-scan reconstruction of the brain cavity confirms an encephalization comparable to that of living strepsirhines (Bush et al. 2004).

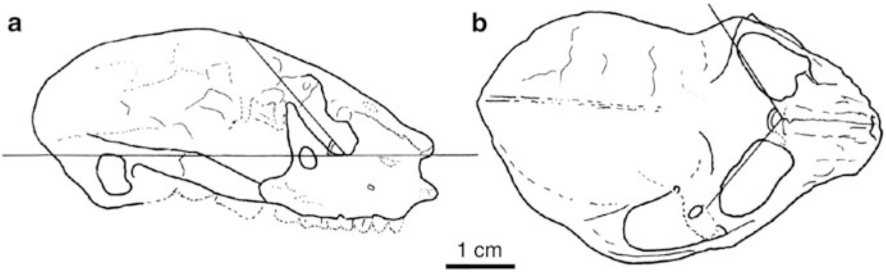

Fig. 29 Schematic drawings of the cranium of *Parapithecus grangeri* in lateral (**a**) and dorsal (**b**) views. It shows the overall elongation of the cranium in lateral view. *Straight lines* indicate the approximate value of the convergence angle (**b**) and the frontation angle (**a**) of the orbits

The complete bullae preserved on the cranium appear relatively distant from each other. They confirm two characters which had been established earlier through the study of isolated parapithecid petrosals: the anular ectotympanic co-ossified with the petrosal around the auditory meatus, and the posteromedial location of the large carotid foramen (Cartmill et al. 1981). The latter study had revealed that there are septa between the promontorium and the ectotympanic. One such septum separates the tympanic cavity from an anterior accessory cavity; the carotid canal travels through this septum, moving for a short distance along the anterior part of the promontorium as a large promontory canal, without a stapedial branch (the perbullar pathway of Cartmill et al. 1981). There is a relatively high degree of petrosal pneumatization, especially of the anterior accessory cavity; a large postglenoid foramen indicates a primitive petrosquamous venous drainage. On the whole, the ectotympanic, pneumatization, and characters of the carotid canal show that parapithecids possessed the distinctive and highly specialized otic complex of living anthropoideans. This morphology bears no resemblance to that of adapiforms. It is in large part shared with *Tarsius* but not with known omomyiforms (Cartmill et al. 1981), and it is a key element at the base of the restricted character-based notion of haplorhines, as endorsed above.

Apidium is a closely related genus, with three species (*A. moustafai, A. phiomense, A. bowni*). It differs from *Parapithecus* by some characters of the dentition. For example, in *A. phiomense*, lower molars increase in size from M/1 to M/3, which is uncommon in anthropoideans; the extremity of their cristid obliqua may be inflated, isolated from the hypoconid by a groove, and forming a centroconid. On the upper molars of *A. moustafai*, the large hypocone is lingually shifted and linked to a thick anterolingual cingulum, which gives the impression that it is larger than the protocone on M1/ and M2/. The anterolingual cingulum can even be cuspidated, resulting in a thick pericone (in *A. phiomense*; Kay and Williams 1994). P2/ is transversely extensive and bears a well-formed paraconule. The upper canines of *Apidium* present an anterior groove which extends into the root (a convergence with cercopithecoids). The highly bunodont teeth of *A. phiomense* would suggest frugivory; however, the species possesses a relatively much thicker enamel than other Fayum primates, and its enamel is of the primitive radial type (not decussating).

A microwear study did not find evidence of hard-object processing (Teaford et al. 1996). Was the diet of this species highly abrasive, and in that case, what was it?

A large sample of postcranials attributed to *A. phiomense* has been studied in detail, which makes it the postcranially best-known Paleogene simian (Fleagle and Simons 1995). The scapula of *Apidium* has a glenoid fossa similar in shape to that of *Saimiri*. It was described by Anapol (1983), who conducted an analysis of scapular angles and the surface of the glenoid fossa, and found the bone to be most similar to those of quadrupedal primates. No humerus shows a complete proximal head. There is a prominent deltopectoral crest, which extends roughly one third of its length. The proximal part is deep anteroposteriorly and narrow mediolaterally. On the distal shaft, the brachialis flange is relatively narrow. There is a large entepicondylar foramen. The articular part shows a relatively small, mediolaterally elongated capitulum, the medial part of which is continuous with the broad trochlea (there is no pronounced groove or lip between them). The trochlea is conical and its medial lip extends further distally than the capitulum. The deep coronoid fossa, the proximal extent of the capitular surface, and the proximal extent of the medial part of the trochlea all suggest that extreme flexion was common in this species. The medial epicondyle is prominent, directed posteriorly at an angle of about 20°, as in arboreal quadrupeds. On the posterior side the trochlear surface is limited by prominent lips, and there is a dorsoepitrochlear pit, a common feature in omomyids and platyrrhines. The ulna has a relatively long olecranon process. The sigmoid cavity, described in detail by Conroy (1976), shows greatest similarity with the platyrrhines *Cebus* and *Saimiri*. The radius presents a head that is oval in shape. Its shaft is very broad and robust in comparison with living primates. Its distal part becomes relatively broad and flattened for a large pronator quadratus muscle, as in arboreal quadrupeds. Its distal articulation shows a sharp styloid process.

Several partial hip bones were recovered (Fleagle and Simons 1979). The ilium shows a broad gluteal plane, rectangular in its preserved part, which is characteristic of anthropoideans, and an expanded iliac plane that narrows proximally, as in *Saguinus*. The ischium is long and proximally broad, and the ischial tuberosity extends slightly above the level of the acetabulum. The dorsal rim of the acetabulum is thicker than the ventral rim. Most characters indicate a quadrupedal primate, although it seems that relative iliac length was lower than in other primates. The femoral head has a rounded articular surface which is restricted anteromedially and expanded posteromedially, as in *Cantius*. Several characters of the femur are typical of leaping primates: a thick and short neck, perpendicular to the shaft; a relatively distal fovea capitis; a prominent intertrochanteric line; a proximal surface of the greater trochanter that is relatively flat and broad in anterior view, anteriorly overhanging the shaft. There is no third trochanter. The lesser trochanter is very large, more rectangular than in living primates, and it joins the greater trochanter to wall off the posterior femoral fossa. The femoral shaft is relatively robust. The distal articulation is higher anteroposteriorly than in all other anthropoideans, and the patellar groove is deep and narrow, bordered by a prominent lateral lip – all characters reflecting a leaping adaptation. The tibia also presents a series of characters associated with leaping:

an extensive, convex lateral condyle and a smaller, concave medial condyle; a proximal shaft that is very narrow mediolaterally; a cnemial crest extending 20–22 % along the shaft, indicating the proximal insertion of the hamstring muscles; tibia and fibula distally appressed for roughly 40 % of their length; a deep medial malleolus and prominent beak on the anterior side, which match the midline groove of the astragalar trochlea, indicating that movements at the ankle joint were restricted to flexion-extension in the parasagittal plane (Fleagle and Simons 1995). The astragalus has a broad dorsal articular surface with pronounced lips and steep sides. The medial trochlear articulation is very shallow, and the fibular facet is steep and relatively shallow. The articular head is ovoid in shape, and its main axis is rotated dorsolaterally. The calcaneum is relatively robust, with a thick tuber and no plantar process. The posterior calcaneal facet is relatively small and very convex, with a steep distal part; the similar size and shape of the matching facet on the astragalus show that there was very little rotation between them at this level. The sustentacular facet is small and circular. There is a prominent peroneal tubercle opposite the sustentaculum. The anterior articular facet faces medially and has little connection with the sustentacular facet, which is unusual and resembles many cercopithecids. The cuboid facet, slightly concave and lunate-shaped, surrounds a deep pit for the calcaneo-cuboid ligament. Below this pit, the tuberosity for the short plantar ligament is more strongly developed than in most platyrrhines. The cuboid is wedge-shaped, broader proximally than distally, and relatively narrow and deep. Its distal face has a single T-shaped facet for one metatarsal, the fourth (MT IV), and the lateral face shows an anterior broad facet for the fifth (MT V). Such a lateral articulation of the fifth metatarsal is unusual among primates; today it is found only in *Tarsius* (Fleagle and Simons 1995). On the navicular, the distal face has three distinct facets for the three cuneiforms, aligned in an L-shaped arrangement as in omomyids, *Tarsius*, and anthropoids (Dagosto 1988).

The bones ascribed to *A. phiomense* show an unusually high variability in size. Few long bones are intact, but the best preserved, completed by others, allow estimations of their median length (e.g., humerus 5.5 cm, femur 8.9 cm). An estimation of the intermembral index gives a score of 62, less than in any other simian and similar to leaping prosimians (Fleagle and Simons 1995). On the whole, *Apidium* shares most characters with small leaping platyrrhines like *Saimiri* or *Saguinus*; however, it was more specialized for pronograde leaping (not VCL), and it also shows a series of other traits – some shared with cercopithecids and others unique among living primates.

The systematic status of Parapithecidae has changed. They have been considered sometimes primitive catarrhines, sometimes platyrrhines, sometimes related to cercopithecoids. Following the detailed analysis of Fleagle and Kay (1987) they have often been considered a primitive sister of all other anthropoideans. However, more recent analyses including Proteopithecidae conclude to an unresolved polytomy between catarrhines, platyrrhines, proteopithecids, and parapithecids (Seiffert et al. 2005b, 2010a). The phylogenetic relationships between these early families and platyrrhines are not yet resolved.

Proteopithecidae and *Arsinoea*

The species *Proteopithecus sylviae* has been found in the locality L-41 of the Fayum. Incomplete dental remains first led researchers to rank it among the oligopithecines; however, the discovery of more complete dental specimens, crania, and some postcranials resulted in revised placement, together with *Serapia eocaena*, in a family Proteopithecidae (Simons 1997a, b; Simons and Seiffert 1999). Members of this family have three premolars above and below. One cranium shows that *Proteopithecus* has spatulate central upper incisors, a relatively large upper canine somewhat transversely compressed, bearing an anterior vertical groove and a lingual cingulum, and upper cheek teeth of large size in relation to palatal breadth. A P2/ smaller than P3/ has only a small lingual lobe with a small protocone and a continuous cingulum. P3/ and P4/ are transversely extended. They both have a strong posterior cingulum which broadens lingually in a shelf reminiscent of the hypocone of the molars. M1/ and M2/ are transversely elongated, have no conule (or only a small paraconule on M1/), a protocone reported to be smaller than the labial cusps, and a relatively large crestiform hypocone. M3/ is reduced. In the lower dentition, P/2 is larger than P/3; both are conical. P/4 is much larger than P/3 and has a large metaconid and a strong lingually recurved preprotocristid, which in occlusal view gives the impression that P/4 has a trigonid similar to that of M/1. It has a short talonid (Fig. 30). The lower molars are generalized, with a trigonid higher than the talonid, which is broad. M/1 has a small paraconid; M/2 and M/3 have a paralophid without cusp. A hypoconulid is frequent on M/1–2, twinned with the entoconid. M/3 is small and shows high variability in its talonid morphology.

The species *P. sylviae* is relatively small; one cranium is 4.4 cm in length. It presents all the simian characters of orbits and auditory region which have been given above for *Parapithecus*, plus a fused metopic suture and lacrimal bone within the orbit (also simian features). Among the distinctive characters of the genus are small premaxillae, large posterior palatine foramina, lack of a posterior palatine torus, and a jugal foramen smaller than in *Parapithecus*. The rostrum is proportionately shorter than in *Catopithecus*, and the anterior margin of the orbit is more forward located, being above a line between P2/ and P3/. The temporal lines converge far posteriorly and join to form a slightly elevated sagittal crest. The latter joins two less distinct nuchal crests and a salient vertical occipital crest. The posterior cresting, more developed than in similar-sized platyrrhines, is probably correlated with the relatively smaller brain size. The glenoid fossa is anteroposteriorly and mediolaterally broad and flat; there is a well-developed postglenoid process and just posteromedially a distinct postglenoid foramen. Both this region and the facing articular process of the mandible are reported as similar to those in *Catopithecus* (Simons 1997a).

Postcranials of *Proteopithecus* include two humeri, a partial femur and hip bone, one femur and two tibiae found in association with a mandible, and an astragalus and a calcaneum (Gebo et al. 1994; Simons and Seiffert 1999; Seiffert et al. 2000; Seiffert and Simons 2001; Gladman et al. 2013). The humerus is very similar to

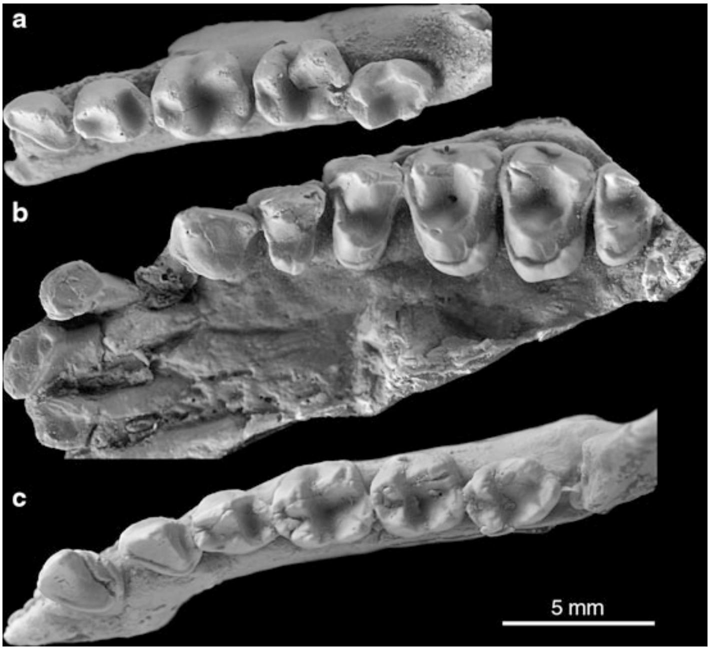

Fig. 30 Dentitions of proteopithecids and oligopithecids. Right mandible of *Proteopithecus sylviae* showing P/3, P/4, and the lower molars (**a**). Partial palate with upper teeth (**b**) and mandible with lower teeth (**c**) of *Catopithecus browni*. The maxilla in (**b**) shows from *left* to *right* the elongated I1/, the shorter I2/ displaced from its broken root, the large and high canine, subtriangular in occlusal view, and the two upper premolars and three molars. On the lower jaw are also preserved the large canine, two premolars, and three molars. Photographs of white-coated epoxy casts, all at the same scale

those of parapithecids. In profile view, its shaft has a distinct sigmoidal curvature. Differences with parapithecids include a less extended supinator crest and less developed brachial flange, narrow and deep bicipital groove (as in *Qatrania fleaglei*), relatively narrow distal articular surface, and broad capitulum confluent with a narrow trochlear surface; on its posterior side the latter shows a well-developed lateral lip within the olecranon fossa. The partial hip bone is similar in many respects to the hip bone of *Apidium*, but has an even larger crest separating the gluteal and iliac planes, and both gluteal and iliac planes are broader in their caudal parts than in *Apidium*. Quantitative ratios used to describe the acetabulum match best with those of extant catarrhines, rather than with platyrrhines or prosimians (Gebo et al. 1994). The femoral neck angle is 108°, and head and neck length are less than in *Apidium*. There is a crista paratrochanterica on the posterior side, between head and greater trochanter. There is a third trochanter at the distal end of the latter, which is more prominent than in any living anthropoidean. The lesser trochanter is large and flange-like. Its lateral crest meets the posterior crest of the greater trochanter, closing the trochanteric fossa as in *Apidium*. However, these crests are less prominent, and the lesser trochanter is less expanded and rectangular, resulting in a trochanteric fossa less extended than in *Apidium*. The trochanteric fossa is interpreted as a more primitive version of that of *Apidium* (Gebo et al. 1994). Distally, the patellar groove is broad and has a prominent lateral lip. The ratio of anteroposterior depth to mediolateral width is 78, lower than in *Apidium* (103). The tibiae are longer and more gracile than those of *Apidium*. Other characters of the proximal part are as in *Apidium* and reflect a leaping adaptation. On the distal part, the fibular articular facet is short (10 % of total length), as in some platyrrhines, contrasting with the long syndesmosis of *Apidium*. The humero-femoral index is 73, higher than in *Apidium* (62). The crural index is 106 (vs. 106–111 in *Apidium*), most similar to those of callitrichines (100–101). The astragalus is very similar to those of parapithecids and small-bodied platyrrhines, but with a lower body and a long axis of the head mediolaterally oriented in distal view (more dorsoplantar in *Apidium*). The calcaneum shows a distal placement of the peroneal tubercle, a distal plantar tubercle, and separated sustentacular and distal astragalar facets – characters which may be shared-derived with parapithecids (Gladman et al. 2013). It also differs from parapithecids in being more slender and in having a greater distal elongation (43 %). Characters of the knee, tibia, and ankle clearly indicate a quadrupedal arboreal locomotion, including frequent rapid running and pronograde leaping.

Proteopithecidae appear to be the most generalized of the African Eocene-Oligocene anthropoideans. They have a large number of similarities with small living platyrrhines, though many of these are considered primitive for simians. It has been suggested repeatedly that proteopithecids are the only serious candidates for a stock from which to derive platyrrhines (Simons 1997a; Simons and Seiffert 1999), because parapithecids and propliopithecids have derived specializations which preclude their playing such a role. However, living platyrrhines also have their own autapomorphies, and until now it has not been possible to identify clear shared derived characters that would ally platyrrhines with proteopithecids. On the contrary, recently found postcranials suggest that proteopithecids may well be more closely related to parapithecids.

The systematic placement of *Arsinoea kallimos*, known only by its lower dentition, has fluctuated. It is a small primate: the complete tooth row of the type mandible, from I/1 to M/3, is less than 2 cm long. Among its distinctive characters are a low-crowned canine, a relatively large, anteroposteriorly elongated I/2, and three simple premolars slightly increasing in size from P/2 to P/4 (Simons 1992). M/2 is reported as low-crowned. There is a large paraconid well separated from the metaconid on M/1, a smaller paraconid close to the metaconid summit on M/2, and no paraconid on M/3. This type of posterior paraconid reduction is unlike what is found in other simians, recalling very different primate groups. *Arsinoea* has been described as “family uncertain,” or found to form a trichotomy with other higher taxa and proposed as member of a new family Arsinoeidae (Simons et al. 2001). More recently, phylogenetic analyses have proposed a place of primitive sister group to other parapithecids (Seiffert et al. 2005a). A closer comparison with *Biretia* would be interesting, and upper teeth would help specify its place.

Catarrhini: Oligopithecidae and Propliopithecidae

For many years, *Oligopithecus savagei* was known only by its type mandible, found in Quarry E of the Fayum. The anterior part of this mandible slightly increases in height anteriorly, and bears a moderate-sized canine with an anteriorly ascending lingual cingulid. There are only two premolars and a P/4 that is relatively short and molarized, with a large metaconid as anterior as the protoconid, and an anteriorly elongated preprotocristid turning lingually into a brief and thick paralophid (almost a paraconid). The P/3 is larger, simpler, and much higher. Its main cusp has a long anterior preprotocristid with wear indicating its honing function for the upper canine. The lower molars are transversely broad, crested with a low relief, with a cristid obliqua reaching the posterior base of the protoconid. M/1 has a small paraconid, and M/2 clearly shows a lingually placed hypoconulid, twinned with the entoconid. The presence of only two premolars, morphologically derived and close to those of *Aegyptopithecus*, makes it a tantalizing catarrhine. However, its molars are quite different from those of the latter, being crested with twinned entoconid and hypoconulid, instead of bunodont with a centrally placed hypoconulid. On the other hand, these molars resemble those of the adapiform *Hoanghonius*, leading to the idea of a status possibly transitional between adapiforms and simians (Gingerich 1977b). This notion was further strengthened by the discovery of an upper molar of *O. savagei* with high crests recalling cercamoniines, interpreted in terms of phylogenetic affinity (Rasmussen and Simons 1988). However, subsequent discoveries, and especially analysis of more complete material of the closely related *Catopithecus*, definitively proved the anthropoidean status of *O. savagei*. A second species of *Oligopithecus, O. rogeri*, was found in the Oligocene locality of Taqah, Oman (Gheerbrant et al. 1995). It completes the knowledge of the genus and shows specific differences. Interesting is the P4/ with a large protocone and well-developed crests forming the lingual part of a trigon (with one labial cusp), and a complete lingual cingulum. The upper molars have an anteroposteriorly more elongated labial part, marked medial waisting, and a thicker and more continuous lingual cingulum, with posterolingual extension on M2/. The trigonid of the lower molars seems less anteroposteriorly compressed.

Catopithecus browni is found in the Latest Eocene locality L-41. Many specimens are known, allowing the description of the dentition, cranium, and parts of the limb skeleton (Fig. 30). The mandibles are anteriorly unfused, a unique case in anthropoideans which suppresses one of their synapomorphies, and also a unique case for catarrhines (Simons and Rasmussen 1996). The lateral incisor is spatulate. The canine is large, projecting, and sexually dimorphic in size. It has a marked cingulid descending anteriorly from the tip and curving posteroventrally on the lingual face. P/3 is also dimorphic. It has a high main cusp and a small talonid. Its preprotocristid serves as honing blade for the upper canine; it is longer in males, which have a broader P/3. P/4 is more complex, with small paraconid and metaconid. The molars are transversely broad. Their crests are not high and their cusps are moderately bunodont. M/1 has a small median paraconid, whereas M/2 and M/3 have a paralophid which seems to enclose the narrow trigonid basin.

The talonid basin is relatively wide, and entoconid and hypoconulid are tightly twinned on all molars. M/3 has roughly the same length but is much narrower than M/1 and M/2; its third lobe is only slightly salient posteriorly. The upper incisors are described and figured by Simons and Rasmussen (1996). They are spatulate and resemble those of small patyrrhines. I1/ is larger and elongated in the mesiodistal plane, and relatively flat on its lingual face, which has a straight margin (Fig. 30). I2/ is smaller and less elongated, with a rounded lingual margin. The upper canine is a simple tooth, transversely compressed, bearing an anterolingual cingulum and an anterior vertical groove, and is dimorphic. P3/ and P4/ are relatively simple, with a large paracone, small styles, the lingual lobe narrower than the labial part, and a continuous thin lingual cingulum at least on P4/. The protocone is smaller on P3/ than on P4/. M1/ and M2/ are relatively simple. Their broad trigon basin is limited lingually by a raised and curved crest, which is formed by a preprotocrista running to the parastyle and a postprotocrista running toward the metacone. A continuous lingual cingulum bears a crestiform hypocone, larger on M2/ than on M1/, and a small pericone on M2/ alone. The labial cingulum is faint and shows a slight mesostyle thickening. M3/ is small, and is reduced in its posterior part.

Six crania of *Catopithecus* are known that are crushed in different ways, allowing many anatomical traits to be recognized (Simons and Rasmussen 1996). In many respects they resemble *Parapithecus* and small extant platyrrhines like *Callithrix*. Thus only some peculiarities are described below. In the facial region, the nasals are broad and long, and the premaxillae have a very broad ascending process. There is a broad interorbital distance, and a broad intercanine distance on the palate. The orbital fissure is made of two parts, an anterior one, which is lenticular, and an inferior one of moderate size. The zygomaticofacial foramen is smaller than in parapithecids and platyrrhines, but larger than in most catarrhines. The relative orbit size indicates diurnality, and convergence is estimated at 120–130°. The anterior margin of the orbit is above the contact between P3/ and P4/, more posterior than in most small platyrrhines. On the ventral side, the palatine bone shows robust pyramidal processes running posterolaterally from the palate, as in *Aegyptopithecus* and some catarrhines; these processes are commonly more gracile in other anthropoideans. On the dorsal side of the cranium, there is no metopic (interfrontal) suture. Strongly developed orbital crests link the posterolateral part of the supraorbital ridges to the temporal lines, which are arcuate and join far posteriorly, bordering a long frontal trigon. The sagittal crest and prominent occipital protuberance suggest a relatively flat and vertical nuchal plane, contrasting with the ballooned shape of small extant platyrrhines. Rough estimates of brain size indicate a low encephalization, even lower than in living prosimians. The relatively large olfactory bulbs project in front of the frontal lobe, as they do in prosimians, whereas they project more downward in extant anthropoideans and *Aegyptopithecus* (Simons and Rasmussen 1996).

Several limb bones have been ascribed to *Catopithecus*. A complete but proximally crushed humerus and two partial distal humeri show that the humerus must have been relatively long; the deltopectoral crest is reduced in comparison with *Proteopithecus*, and the brachial flange is moderately developed. The entepicondylar foramen is smaller and more medially placed than in *Apidium*; it is lost on one of the three specimens; its lateral wall is confluent anteriorly with the medial edge of the trochlea. A large medial epicondyle projects more medially than in other Fayum taxa. On the articular part, the capitulum is very round and sharply demarcated from a long and prominent capitular tail. Compared with *Apidium*, the capitulum and zona conoidea are relatively shorter, whereas the trochlea is broader. The angle of translation of the ulna is small, as in other Fayum primates, whereas it is larger in platyrrhines (Gebo et al. 1994; Rose 1988). A morphometric study of the distal articular surface shows that this surface is phenetically closer to those of propliopithecines than to those of other Fayum anthropoideans (Seiffert et al. 2000). The femur has a relatively short head and neck length, a head more rounded than in *Proteopithecus*, and a notch between the greater trochanter and the head that is shorter and deeper than in *Apidium*. A third trochanter extends farther distally than in *Proteopithecus* and appears variable, ranging from prominent to poorly developed (Seiffert and Simons 2001). The large lesser trochanter does not contact the long trochanteric crest, which runs distally. The astragalus of *Catopithecus* is very different from those of parapithecids and proteopithecids. It has an increased curvature of the distomedial margin of the trochlea, a relatively deep and medially projecting cotylar fossa, and an elevated lateral trochlear rim and increased trochlear wedging (anterior broadening). It also exhibits a laterally projecting fibular facet, a mediolaterally broad head, a low medial body, and a relatively wide distal half of the ectal facet. These limb bones suggest that *Catopithecus* moved more deliberately and climbed more frequently than the smaller parapithecids and proteopithecids. The astragalus reflects an emphasis on inverted and abducted foot postures, as well as powerful hallucial grasps. As with *Aegyptopithecus*, which it resembles, this astralagus may indicate regular hindlimb suspensory behavior.

The recent description of *Talahpithecus parvus*, from the late Middle or Late Eocene of Dur At-Talah in Libya, proves the existence of very small and highly crested oligopithecines (Jaeger et al. 2010). As mentioned above, the dental characters of *O. savagei* first led researchers to hesitate between catarrhine and adapiform affinities. After its anthropoidean status was clearly established, the task remained to assess whether the highly crested oligopithecines had been a primitive sister group of the bunodont (parapithecids + propliopithecids), with convergence in the anterior part of the dentition, or whether they were more closely related to the propliopithecids. Postcranials found subsequently have added a considerable amount of evidence in favor of the second view. The differences in molar morphology, which had previously impressed many scholars, can now be explained by a process of upper molar crest increase associated with a reduction of hypocone and lingual part, as seen in sivaladapids (Seiffert et al. 2004). Thus the loss of P/2 and the similarity in premolar morphology, instead of being convergences, probably reflect the close affinity of oligopithecids and propliopithecids. The presence of solely two premolars remains a hallmark of the catarrhines (and sometimes the oligopithecines are considered a subfamily of the propliopithecids, a possible choice).

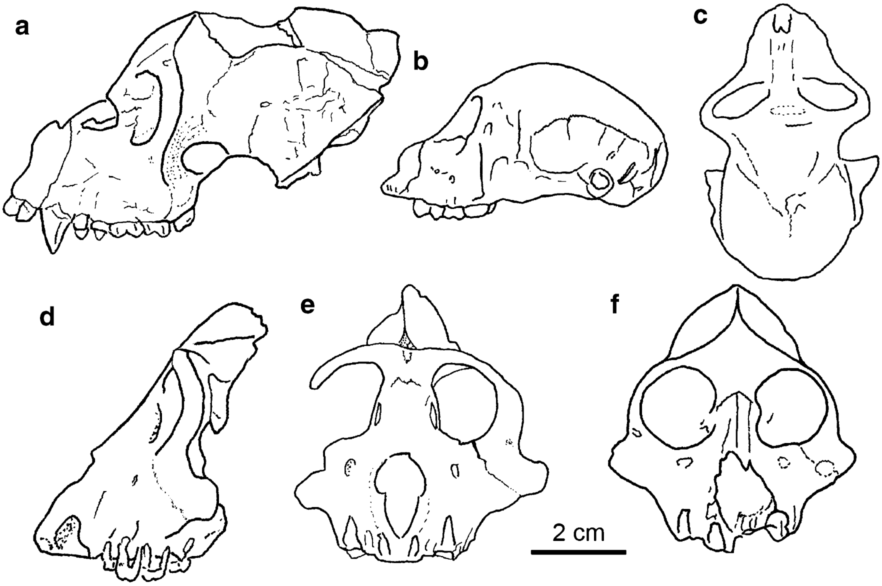

Fig. 31 Schematic drawings of several crania of *Aegyptopithecus zeuxis*. (**a**) is the male cranium reconstructed with some possible deformation of the muzzle, (**b**) is the undistorted cranium of a female, and (**c**) is the dorsal view of the same; (**d**–**f**) are two other faces of males, one in profile (**d**) and anterior (**e**) views, the second only in anterior view (**f**). The extreme sexual dimorphism present in this species can be seen through the size difference between the female (**b** and **c**) and the males and also through the absence of sagittal and nuchal crests in the female. All these crests are present in (**a**), and a strong variability in the development of the sagittal crest can be seen among the males

The family Propliopithecidae, known only in the Oligocene until now, includes the genera *Aegyptopithecus, Propliopithecus*, and *Moeripithecus*. The best-known species by far is *A. zeuxis*, known by many skulls and several postcranial elements from quarries I and M of the Fayum. A cranium of a young male, found in 1966, has been described and depicted many times (e.g., Simons 1967, 1972; Szalay and Delson 1979). It has a relatively long muzzle (Fig. 31), orbits with a slight dorsal orientation in lateral view, tooth rows with a slight posterior divergence, etc. However, this cranium had been reconstructed from a fossil that had been shattered in its facial region. The later discovery of several nondistorted partial male crania brought to light some distortion in this first reconstruction, as well as very high morphological variability (Simons 1987). Comparison of four male crania revealed enormous differences between them: development of the sagittal crest from very low and starting somewhat posteriorly, to very high and shifted anteriorly just behind the orbits (Fig. 31); orbit orientation, in profile view, from slightly turned dorsally to vertical; zygomatic root and suborbital height, from moderate to stronger and much higher. These differences accompany differences in age as visible from tooth eruption and wear. They are themselves attributed to aging, with enlargement of the temporal ridges due to growth of the temporalis muscle and

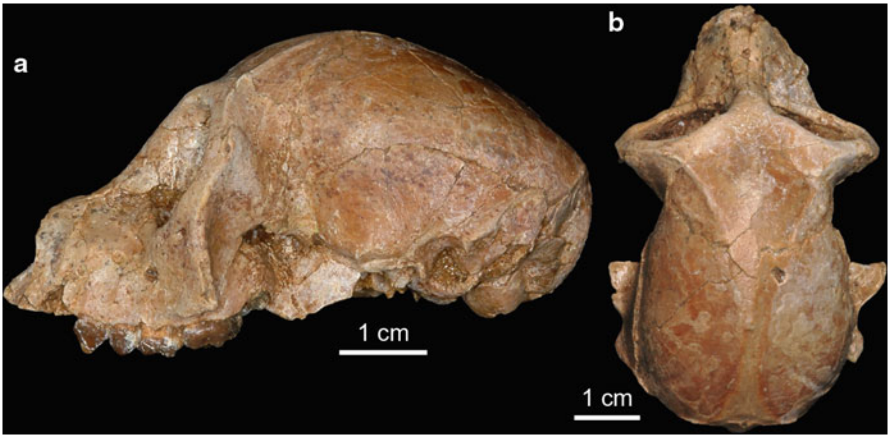

Fig. 32 The undistorted cranium of a female *Aegyptopithecus zeuxis* from the Fayum, Egypt, in lateral (**a**) and dorsal (**b**) views at slightly different scales. This is the only specimen showing the exact relationships between face and braincase in this species (Courtesy of, and copyright by, P. D. Gingerich)

even deepening of the face. Aging also produces differences in ventral view: zygomatic arches mainly above M2/ in young individuals, and above M3/ in older ones; posterior concavities of the palate between M2/ and M3/ in a young male, and well posterior to M3/ in an old one (all indicating an anterior shift of the cheek teeth with age). These differences are further accentuated when males are compared with females, a small individual of which was subsequently described (Simons et al. 2007). The female specimen is minimally damaged and is the only cranium showing the exact placement of the braincase relative to the face in *Aegyptopithecus* (Fig. 32). An angle of 150–160° is measured between the plane of the palate and that of the basioccipital. Several quantitative analyses of tooth dimensions have been done to see if two species could be distinguished in the assemblage from the two quarries; however, until now they all conclude to one species with high cranial variability (Kay et al. 1981; Simons et al. 2007). In fact, *A. zeuxis* reveals for the first time in the Paleogene a sexual dimorphism affecting not only canines and cranial superstructures, but also the size of the postcanine dentition – something found to be the case in only the most dimorphic extant species.

Among other noticeable features of *Aegyptopithecus* are its moderate rostrum length, anteriorly concave nasofrontal region in profile view, and broad interorbital region with a convexity in the medial orbital wall, resembling African great apes; the orbital convergence is 130–135°. The angle of divergence between the tooth rows is 12–13°. The characters of the otic region are those of anthropoideans as seen in parapithecids. However, the lateral pterygoid wing does not contact the auditory bulla. On three specimens, the dorsal part of the ectotympanic extends out in a process, suggesting the incipient development of a tubular ectotympanic (Simons et al. 2007). The use of micro-CT-scan has produced images of the endocast, as well as much better estimates of endocranial volumes than the previous ones: 14.6 cm^3 for the female, instead of the earlier 27 cm^3 for a comparable female cranium (Simons 1993); a new estimate of the young male endocranial volume, 20.5–21.8 cm^3, is again lower than the earlier estimation of 27 cm^3 by Radinsky (1977). The authors conclude that encephalization in *Aegyptopithecus* was very low, "at best strepsirhine-like, and perhaps even non-primate-like" (Simons et al. 2007), although the range of body size estimates is broad. Further scrutiny of body weight should allow more precise estimates of the brain-to-body mass relationship.

The dentition of *Aegyptopithecus* is well known. The two upper incisors are spatulate and have a complete lingual cingulum. I1/ is much larger than I2/ and has a lingual cingular bulging. The robust canines, much larger in males than in females, have an anterior vertical groove and a lingual basal cingulum. The cheek teeth are quite bunodont. The two premolars are subequal in size, bicuspid, and have an almost complete lingual cingulum. The anterolabial part of P3/ can be salient in males. The molars have moderately low and rounded cusps. M2/ is much larger and much more transversely elongated than M1/. The trigon is well formed, with preprotocrista going toward the anterolabial corner and postprotocrista going toward the metacone summit, forming a complete crista obliqua. On M1/ and M2/ the large hypocone is almost as high as the protocone, and linked to a complete lingual cingulum. The M3/ are highly variable. The two mandibles of *A. zeuxis* are high, robust, solidly fused anteriorly, and anteriorly increase in height in males. The incisors are relatively small and narrow, and moderately proclive. They have an elongated crown and a mesial cingulid (seen on DPC 1112). I/2 is slightly larger than I/1. The lower canine is high and pointed, more gracile than the uppers. Its lingual cingulid runs from the posterior base of the crown, curving and ascending toward its tip. The two lower premolars are different. P/4 is short and molarized, with a metaconid almost as high and as anterior as the protoconid; it has an arcuate paralophid, and a small talonid basin limited by a low hypoconid and a subhorizontal postcristid. P/3 is higher and more pointed. Its height in lingual view is underlined by a deep ventral expansion of the posterior cingulid, followed by a continuous anterodorsal ascending course of the cingulid. This difference is accentuated on the P/3 of males, which are larger, higher, and more pointed, and which have a longer preprotocristid for honing with the upper canine. The lower molars differ from those of oligopithecids by some features: absence of a paraconid on M/1, increased bunodonty, transversely broader M/2, M/2 larger than M/1, well-developed posterior cingulid, and a more centrally located hypoconulid, leaving space for a small valley or fovea between entoconid and postcingulid. M/3 is larger than M/2; it is essentially made longer through its much larger, and quite variable, hypoconulid.

Among the Fayum primate limb bones studied by Conroy (1976), one ulna was referred to *Aegyptopithecus*. It was found similar to that of *Alouatta*, the extant howler monkey. Several other bones were subsequently described; a summary of those attributed both to that genus and to *Propliopithecus* was given by Gebo (1993). The humerus of *Aegyptopithecus* is robust and shows strong muscle crests, especially the deltopectoral, and the brachial flange is more laterally extended than in any other anthropoidean. Among the characters which indicate arboreal quadrupedalism are the prominent and laterally placed tubercles bordering the posteriorly facing head, a slight flattening on the top of the head, and the very distal crest for the teres major muscle. There is a wide medial epicondyle (strong flexors), a dorsoepitrochlear fossa, and an entepicondylar foramen. On the distal articular surface, the capitulum is round and has a small capitular tail, the trochlea is relatively wide, the zona conoidea wide and shallow. The olecranon fossa, which is shallow, is one more primitive/quadrupedal feature, whereas the articular surface is of the nontranslatory type as in other catarrhines (Rose 1988; Gebo 1993). Most characters of the ulnae also indicate arboreal quadrupedalism: robust bone, proximal convexity, a relatively long olecranon and low coronoid processes, and a broad and shallow sigmoid notch with oblique orientation of the flexion-extension axis. The prominent pronator crest indicates climbing capabilities. The femur of *Aegyptopithecus* is a very robust bone, which retains a third trochanter (or gluteal tuberosity) – a character independently lost in the parapithecids and later catarrhines (Ankel-Simons et al. 1998). The tibia of *Propliopithecus chirobates* is short and robust, exhibits asymmetrical condyles, and shows a distal articular surface similar to those of Early Miocene proconsulids (Fleagle and Simons 1982). The astragalus of *Aegyptopithecus* shows a relatively long and moderately high body, and a short neck angled medially. The trochlea is asymmetrical, with a higher lateral rim, as well as a medial rim anteromedially curved above a deep medial malleolar cup (cotylar fossa), which produces abduction associated with dorsiflexion of the foot. The fibular facet projects quite far laterally, as in *Catopithecus*. The calcaneum is very broad mediolaterally in both *Aegyptopithecus* and *Propliopithecus*. Its plantar surface is slightly concave anteroposteriorly, and its proximal part slightly bent medially. Its distal part is moderate in length (38 % of total length). It exhibits an elongated posterior facet and an anterior extension of the sustentacular facet, both indicating extensive rotation and sliding of the astragalus on the calcaneum. Distally, a deep pivot indicates high rotational capacities. The first metatarsal is relatively long, curved, and possesses a relatively short peroneal tubercle, as in other anthropoideans. It presents a facet for a prehallux, a primitive character; two other metatarsals also present primitive characters on their narrow proximal part (Gebo and Simons 1987). A long, slender, and moderately curved proximal phalanx is typical of climbers. On the whole, most characters suggest arboreal quadrupedalism and climbing similar to *Alouatta*; increased foot mobility and strong hallucial grasping possibly reflect frequent suspensory feeding postures, as in the latter.

Other species and genera of propliopithecids include three species of *Propliopithecus*, *Moeripithecus markgrafi*, and an unnamed propliopithecid from Taqah, Oman. The three species of *Propliopithecus* are smaller than *A. zeuxis*, and they differ from it by a series of dental characters: lower crowned lower incisors, lower molars with a well-developed labial cingulid, more peripheral cusps and straight-sided crowns, and a transversely broader M1/. *P. haeckeli*, coming from an unknown level and described long ago (Fig. 33), is considered more primitive than

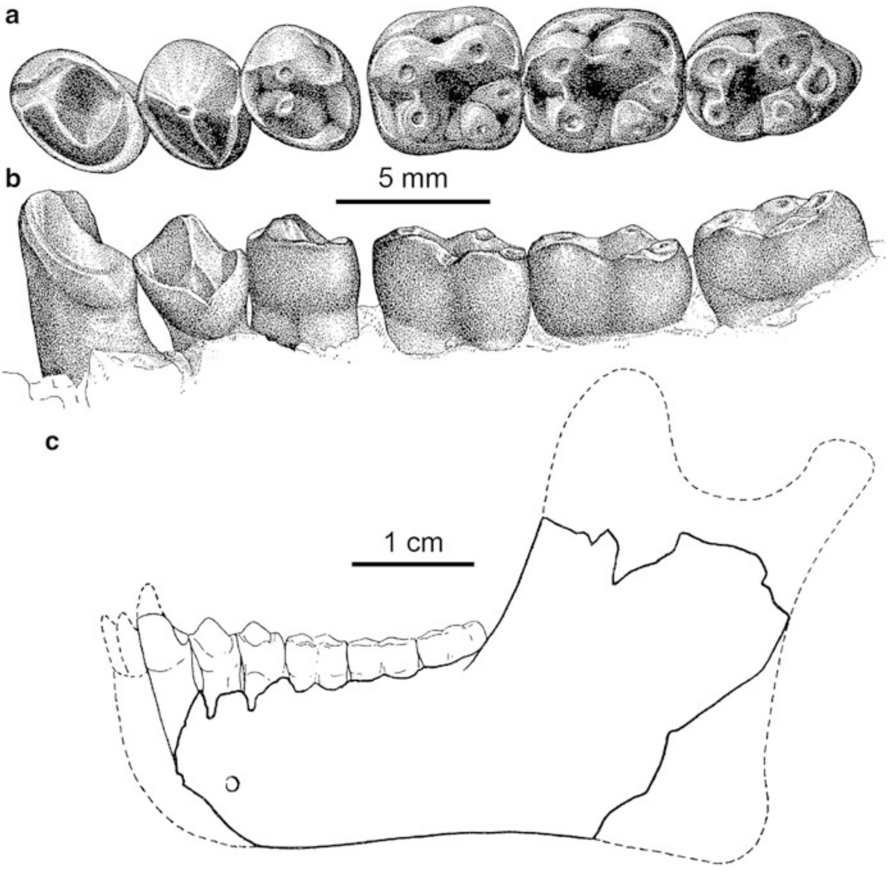

Fig. 33 Right lower dentition in occlusal (**a**) and lingual (**b**) views and reconstruction of the lateral view of the mandible of *Propliopithecus haeckeli* at two different scales (From Kälin 1961)

the larger *P. chirobates*, known by samples from Quarries I and M of the Fayum (Schlosser 1911; Kay et al. 1981). *P. ankeli* from Quarry V is even larger and has transversely very broad lower molars. The type and only known specimen of *Moeripithecus markgrafi* is also an early find without precise stratigraphic provenance. It is a partial mandible with M/1 and M/2, showing a unique combination of characters. The molars have a strong basal crown inflation and a transversely short talonid basin; they are more crested than in other propliopithecids, and their twinned entoconid and hypoconulid recall oligopithecids. Treated for many years as a species of *Propliopithecus*, *M. markgrafi* is now recognized as a valid genus with probable transitional significance. In a similar vein, a better documented Oligocene species from Taqah, Oman, was first described as pertaining to *M. markgrafi*, but in recent years specialists have tended to consider it a distinct taxon – one also presenting characters that are primitive for propliopithecids (Thomas et al. 1991; Seiffert et al. 2010a). Whereas the lower dentition is close to those of other propliopithecids (a male has an enormous P/3), the upper molars are more transversely elongated and show much smaller hypocones, which are clearly primitive characters. The Taqah species, large and Oligocene, underlines the diversity of propliopithecids, which likely deserve the distinction of a fourth genus.

Systematic interpretations of the propliopithecids, mainly *Aegyptopithecus*, have changed dramatically through time, due to the discovery of more complete fossils and the increasing role of locomotor characters for primate phylogenetic reconstruction. The partial dentitions that were found first could reasonably be compared with those of living great apes. Discovery of the skull revealed the primitive, platyrrhine-like state of the ectotympanic. An entepicondylar foramen found on the humerus was also a primitive feature. These two characters prevented placement of *Aegyptopithecus* among crown catarrhines; however, a frequent move was to include *Aegyptopithecus* as a primitive catarrhine because it had only two premolars, and to modify the defining characters of the group accordingly. However, within the catarrhines, classifying *Aegyptopithecus* as a hominoid implied that the two characters at issue had evolved convergently in hominoids and cercopithecoids. For example, Simons (1987) insisted that the similarities shared by *Aegyptopithecus* and the great apes (deep face, temporal cresting, broad lacrimals and interorbital region) were shared-derived and implied a hominoid status for the propliopithecids. However, a more detailed study of the interorbital region and the distribution of its characters concluded that it would be more parsimonious if an African ape-like system of the ethmofrontal sinuses were the primitive condition for crown catarrhines (Rossie et al. 2002). *Aegyptopithecus* and probably *Proconsul* also were considered primitive sister groups of a clade (cercopithecoids + hominoids). The latter view has gained general support based on consideration of locomotor adaptation and associated characters: pronograde arboreal quadrupeds such as *Aegyptopithecus* preceded the more lightly built and tailless proconsulids, which themselves preceded the adaptive divergence of semi-terrestrial cercopithecoids and orthograde arboreal hominoids. Propliopithecids are primitive catarrhines, and likely a primitive sister group of crown catarrhines. They include the ancestors, or good approximates of the actual ancestors, of Miocene–Recent catarrhines. As such they are one of those indispensable paraphyletic taxa that are needed if evolutionary history is to be reconstructed.

The First Proconsuloid

At the end of the Oligocene, a large catarrhine of more modern aspect is found in Kenya. *Kamoyapithecus hamiltoni* is known by dental and gnathic remains only. It is a large animal; the length of its upper tooth row is roughly 1.5 times that of *Aegyptopithecus zeuxis*. The species is documented by a maxilla bearing P4/–M3/, the tip of an upper canine, an anterior mandibular fragment, and an I/2 (Leakey et al. 1995). Its cheek teeth are bunodont, low-crowned, with moderate labial and lingual flaring. P4/ is oval in outline. M2/ is only slightly larger than M1/ and has roughly the same size as M3/. The molars are transversely broad in comparison with

Later Miocene proconsulids, but quite short and square in comparison with propliopithecids. A large hypocone is close to the protocone, present and slightly smaller on M3/ than on M1/ and M2/. The cingulum is not crenulated. The large robust upper canine may be a derived character shared with later forms, as is the position of the hypocone. The very well-developed superior mandibular torus is also found in large-size *Proconsul* species. As seen with the upper molar proportions, *K. hamiltoni* in many ways appears intermediate between earlier propliopithecids and Later Miocene–Recent catarrhines. It can be considered a primitive member of the informal proconsuloids.

Anthropoidean and Platyrrhine Origins, Afrotarsiidae, and Further Phylogenetic Questions

Platyrrhine Origins

Before discussing anthropoidean origins, it is necessary to envisage the origin of the Platyrrhini, the South American monkeys. They are documented in Bolivia in the "Salla Beds," Salla-Luribay Basin, which were long believed to be Early Oligocene (Hoffstetter 1969). However, the Deseadan land mammal age was subsequently redated, and the Salla Beds are now considered Late Oligocene, or Oligo-Miocene (an age of 25–26 Ma is often mentioned). The genus *Branisella* with its only species *B. boliviana* is documented by dental material (Fig. 34). The upper cheek teeth are moderately bunodont; the lower ones are also clearly high-crowned. The roots indicate that P2/ was small. P3/ and P4/ have a well developed lingual part, with large protocone. On P4/, the protocone has a postprotocrista continuous toward the posterolabial part; there is a transversal groove between protocone and paracone, and a continuous and thick lingual and posterior cingulum. The upper molars have the three usual main cusps. It seems that the crista obliqua is sometimes interrupted by a transverse groove. There are important variations in the extension of the lingual cingulum and hypocone, leading to a triangular or more rectangular lingual outline. This led to the initial distinction of some specimens as another taxon *"Szalatavus multicuspis,"* but further specimens showed that these differences reflected high intraspecific variations (Rosenberger et al. 1991; Takai and Anaya 1996; Takai et al. 2000). M3/ is smaller than the other molars and can have a very reduced metacone (variable). The mandibles are fused and the dental arcades are close to a V. I/2 is larger and set more posteriorly than I/1. It has a complete lingual cingulid. The canine is oval in outline, with its longitudinal axis bent anterolaterally; it bears a continuous lingual cingulid. P/2 is not reduced. It has roughly the same size as P/3, is unicuspid, and bears a strong lingual cingulid, curving into a posterior one labially ascending toward the main summit. P/3 has a well-formed metaconid, lower and posterior to the protoconid, whereas P/4 has a metaconid roughly as high and as anterior as the protoconid. P/4 also has a small talonid. The three lower molars are transversely broad, with long labial slopes resulting in transversely short trigonid and talonid basins (Fig. 34). Their anterior

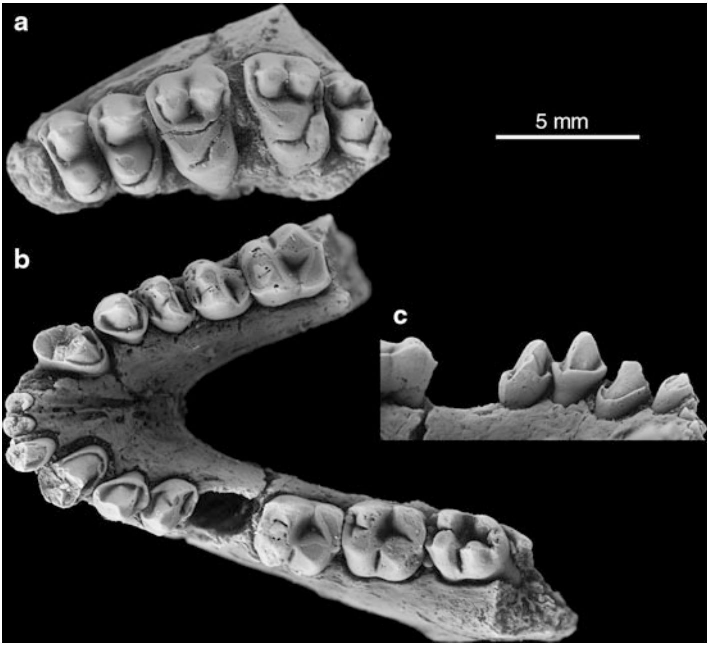

Fig. 34 Dentition of *Branisella boliviana*. Maxilla with two upper premolars and three molars in occlusal view (**a**). A lower jaw with fused symphysis, preserving the anterior teeth, three premolars on the *right* side and the three molars on the *left* side, in occlusal view (**b**) and lingual view of its left anterior teeth P/3, P/2, and partial canine and I/2 (**c**). Photographs of white-coated epoxy casts, all at the same scale

paralophid is transverse and continuous; there is almost no labial cingulid, only a basal closing of the labial trough between protoconid and hypoconid. M/3 is especially short posteriorly; a hypoconulid may be identified on its rounded postcristid, but there is no third lobe.

Branisella is evidently the oldest known platyrrhine. It is sometimes considered as a good ancestral morphotype for them; or as more closely related to one living lineage, implying an earlier diversification (e.g., relatedness to callitrichines for Takai et al. 2000); or, more commonly, as an early primitive sister group of all other platyrrhines. All specimens found in the Salla Beds show strong dental wear, and it has been suggested that their high-crowned lower molars were an adaptation to an abrasive diet, probably related to the semi-arid environment revealed by the fossils and geology of these beds. Therefore, the likely existence of other taxa living in contemporaneous humid and forested areas has been postulated. Whatever its relationships with later platyrrhines, *Branisella* testifies that the group was present in South America by the Late Oligocene. Concerning its origins, all specialists agree that South American platyrrhines must have a common origin with African catarrhines – but when and where? Close affinity between the two groups suggested to Hoffstetter (1972) and others an African origin and subsequent dispersal to South

America. However, a scenario of primates rafting over the Atlantic Ocean, which was already wide at the time, has often met with considerable skepticism (e.g., Conroy 1976). Alternatively, a common source on northern continents and subsequent dispersal to Africa and through North America to South America has been advocated – a proposal sometimes revived in conjunction with putative Asiatic anthropoideans (eosimiids and amphipithecids). However, as seen above and discussed further below, this Asiatic origin is not only far from established, it appears unlikely. With respect to the platyrrhines, it would imply a dispersal through North America – a continent with a rich and continuous fossil record, and yet one in which no suitable ancestor has ever been found. Furthermore, exchanges between the two Americas were interrupted between the Paleocene and the Plio-Pleistocene. This dispersal route for primates thus appears extremely unlikely. On the contrary, new finds in Africa have revealed that the proteopithecids were relatively close to the platyrrhines. *Branisella* and *Proteopithecus* both share the unusual combination of a reduced P2/ and unreduced P/2 (Takai et al. 2000). As seen above, *Proteopithecus* cannot yet be ranked among the platyrrhines. There is still a morphological gap between known African Eocene fossils and platyrrhines, although a common origin is the most consensual view. It is paralleled by the stronger case of an African origin for the South American caviomorphs. A chance dispersal from Africa to South America is thus postulated (Holroyd and Maas 1994). It probably implied the conjunction of several factors: intermediate land on the Mid-Atlantic ridge, a sea-level drop, the rafting of small animals able to survive seasonal food shortage, etc. If this is what occurred, African platyrrhines or stem platyrrhines should be found. It is a real possibility, given that all African anthropoideans named to date come from North Africa and Arabia, leaving the possibility that other groups lived in more southern regions (see below on intriguing fossils found in Namibia).

Anthropoidean Origins and Postcranial Characters

Anthropoidean, or simian, origins have been a field of lively debate during the last two decades. This field has become progressively polarized between three hypotheses: first, a hypothesis rooting the anthropoids in Eocene adapiforms; second, a more commonly adopted hypothesis linking them to the two Asiatic families Eosimiidae and Amphipithecidae; and third, a hypothesis of ancient origin in Afro-Arabia. On the whole, the Fayum anthropoid evidence of three distinct clades differentiated by the early Late Eocene and the implications of platyrrhine origins for a fourth clade jointly provide sufficient evidence to allow researchers to infer a long undocumented history of early simians in Africa, unless the Asiatic connection turns out to be true. As the Paleocene *Altiatlasius* (see below) is found to have possible simian characters, it reinforces the possibility of an ancient African differentiation for the group.

Can an adapiform ancestry be defended? This old hypothesis was revived by the discovery of similarities existing between teeth and dentaries of cercamoniine and hoanghoniine adapiforms, on the one hand, and those of oligopithecids, on the other (Gingerich 1975, 1977b). It was further advocated in studies of both adapiforms (Rasmussen 1990) and Fayum anthropoideans (Simons 1987; Simons and Rasmussen 1996). It was adopted in a study of Messel adapiforms (Franzen 1994) and further argued for in the recent study of *Darwinius*, supposed to be a haplorhine (Franzen et al. 2009). However, the discovery of oligopithecid crania showed that the dental similarities invoked earlier were in fact convergences. As mentioned above, key characters of the auditory region emphatically rule out the adapiform hypothesis (Cartmill et al. 1981). The key haplorhine cranial characters cannot be checked on *Darwinius* because its cranium is crushed; however, *Darwinius* is certainly a cercamoniine adapiform, and in this group the well-preserved skull of *Pronycticebus* shows that they are strepsirhines and certainly not haplorhines. Difficulties linked to the haplorhine concept (*Tarsius* + simians) have been mentioned above. If they were to lead to a view of convergence instead of homology for haplorhine characters, this would not be in favor of the adapiform view, but rather in favor of a third group yet to be identified.

The Asiatic connection could imply multiple dispersals between Asia and Africa. For example, the schema arrived at by Beard et al. (2009) allies eosimiids with African simians and suggests a closer phylogenetic link between amphipithecids, propliopithecids, and platyrrhines. This implies two dispersals, one for eosimiids, and a second one for amphipithecids in either direction, return to Asia in their schema or second dispersal to Africa with a less parsimonious tree. As seen above, amphipithecids cannot be close to propliopithecids, and a more consensual schema would imply one dispersal of an eosimiid giving rise to the African simian radiation (Williams et al. 2010). This is a real possibility (Fig. 36). However, it implies that the Shanghuang petrosal attributed to an eosimiid by MacPhee et al. (1995) be ascribed to an omomyid instead (Kay et al. 1997), which may appear unlikely. That hypothesis is partly sustained by postcranial characters, which have been interpreted as shared-derived between eosimiids and anthropoideans. This requires a critical look.

As indicated above, the Shanghuang fissure fillings have yielded not only eosimiids but a series of four morphological groups based on tarsal characters (Gebo et al. 2001). Study of the calcanea allows their placement along a morphocline between small primates with short and broad calcanea, adapted to quadrupedalism and climbing (“protoanthropoids: new taxon”), to markedly elongated calcanea, adapted to leaping (“prosimians: tarsiids”). Intermediates are the “protoanthropoids: eosimiids,” which are slightly broad, and the “prosimians: unnamed haplorhines,” which are narrow and very omomyid-like (Fig. 35). Astragali complete the tarsal characters of these four groups. The locomotor diversification between these groups took place among tiny Middle Eocene primates of the same region in China, in the presence of a larger omomyid (*Macrotarsius*) and a larger and more climbing-adapted adapid. Is it reasonable in such a context to hypothesize that some of these small primates would be in the process of reversal from a prosimian-like leaping (omomyid-like, not extreme) to quadrupedalism? This change would have had to be so marked that a medial tibial facet extended to

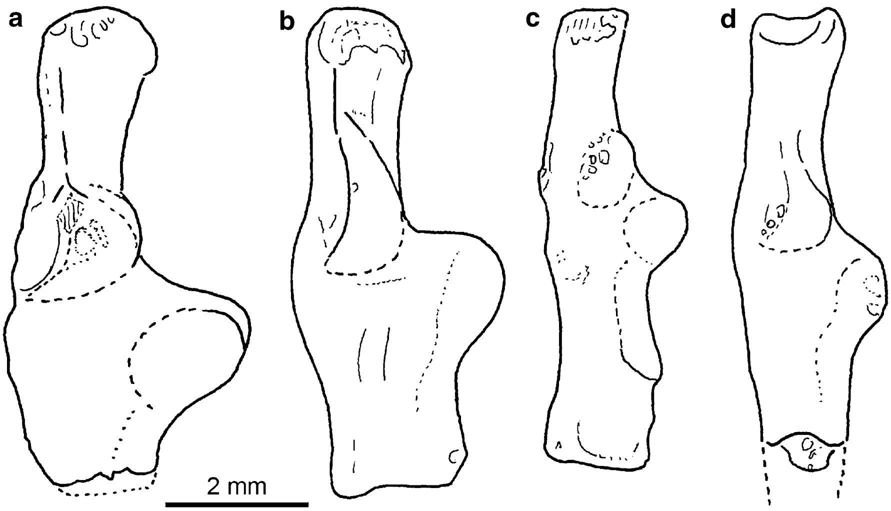

Fig. 35 Schematic drawings of the four types of calcanea identified by Gebo et al. (2001) in the Shanghuang fissure fillings, all in dorsal view. They constitute a morphocline from a broad and short morphology typical of generalized arboreal quadrupeds (**a**) to progressively narrower and more elongated calcanea until the extremely elongated one in (**d**), which reflects a high leaping specialization. (**d**) is ascribed to a tarsiid, (**b**) to an eosimiid; (**c**) appears omomyid-like or cheirogaleid-like in proportions. This morphocline can also be most simply interpreted from primitive in (**a**) to most derived in (**d**). In this case, the anthropoid-like proportions in (**a**) would not imply phylogenetic affinity with simians but only primitiveness among primates

the ventral border of the astragalus would retract to a more dorsal position – something that can hardly be explained in adaptive terms. Much more parsimonious is the view that, because a reduced medial facet is primitive in primates, quadrupedalism was the likely primitive primate locomotor mode (or, if a component of leaping was present, it was low or recent enough to have led to some long bone lengthening as in *Archicebus*, but not yet to medial astragalar and to tibial modification). This fits with the notion of short and broad calcanea as probably primitive in primates, as indicated by extra-group comparisons, reinforcing quadrupedalism and climbing as primitive in the group. Several degrees of leaping were successively reached by different groups, with probable parallelisms between them (such convergent evolution is demonstrated among living primates by the fact that VCL specialists have evolved convergently in at least four families of extant primates). Increasing specializations are expected during evolutionary radiations. Reversals can happen, but usually only under special conditions (further adaptive transitions). Under these assumptions, the anthropoidean-like tarsals of Shanghuang in large part retained postcranial characters that are primitive for primates. They do not prove anthropoidean affinities. This also applies to the astragali of amphipithecids from the Pondaung Formation (Marivaux et al. 2003, 2010; Dagosto et al. 2010). Eosimiid tarsals are probably not primitive for all their characters. For example, might their high astragalar neck angle be convergent with

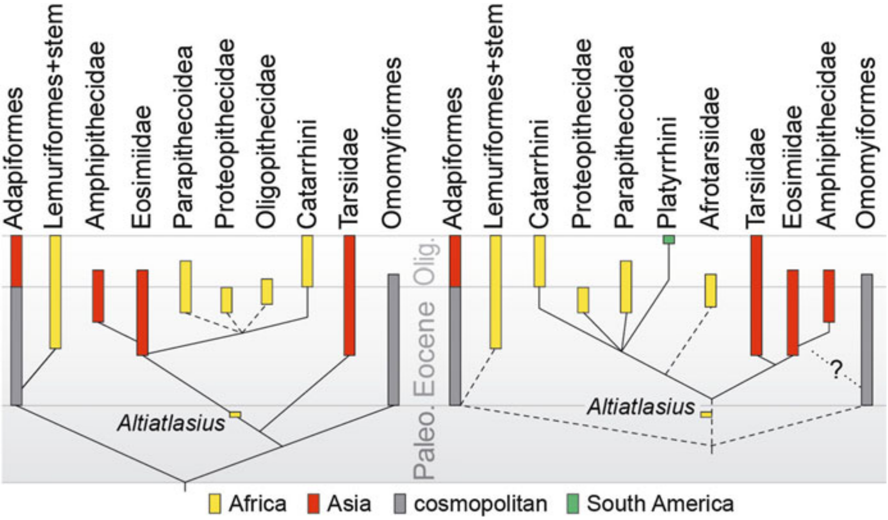

Fig. 36 The two main current hypotheses of anthropoid origins. *Left* is one of the consensual views emerging from the cladistic analyses of large data sets supported, for example, by Williams et al. (2010). In this schema, African simians are rooted in early Asiatic Eosimiidae, which are considered simians or stem-simians having no close relationship with tarsiids. *Right*, another view, considered more likely here, implies a longer history of early African simians with a probable African origin of the typical anthropoid characters. In this case, Eosimiidae and possibly Amphipithecidae could be related to tarsiids in an extended tarsiiform radiation (however, some of the taxa included here might also appear as derived omomyiforms as indicated by ?). Both hypotheses preserve a haplorhine clade, stem-based and extended to include omomyiforms in Williams et al. (2010), more restricted and character-based here. If Tarsiidae themselves appeared rooted in omomyiforms, anatomical haplorhinism would have lost any phylogenetic meaning and reflect only a convergence in cranial adaptation

that of adapiforms? The peculiar cuboid facet, with its removed articular wedge, is clearly derived. However, analogous modifications of the cuboid facet have been described, for example in adapines and amphipithecids (Godinot 1992a; Ciochon and Gunnell 2004). A more detailed study of this facet in many groups is needed, including functional aspects, to decipher homologous and convergent changes. At present, the anthropoidean affinities of eosimiids based on tarsal characters do not appear convincing.

The significance of the anthropoidean postcranium is an old problem. Anatomists have recognized for a long time that living simians are generally more primitive in their postcranial anatomy than living prosimians. Small simians do not show the degrees of specialization reached by some prosimians for leaping or for hand and foot powerful grasping. Because for dental and cranial anatomy there is evidence that early simian characters evolved from prosimian characters, many authors since Gregory (1920) have assumed a similar scenario for postcranial anatomy. This model, Model 1 of Dagosto (1990), implies the reversal of a whole suite of characters – of the knee joint, the first metatarsal joint, the tarsals, etc. Other scholars have considered it more likely that anthropoideans retained their primitive postcranial characters from the euprimate morphotype (Ford 1988; Godinot 1992b). Dagosto's Model 1 explained these reversals through an emphasis on above-branch quadrupedalism, which could have accompanied a marked increase in size. Indeed, at the time when this model was proposed, known fossil anthropoideans were larger than most early fossil prosimians. Strangely, the same scenario of reversals has been maintained for the extremely small eosimiid fossils discovered more recently in China (Gebo et al. 2000, 2001). However, their Middle Eocene age and extremely small size render such a scenario questionable – and quite unparsimonious, as seen above for the tarsal characters (and as could be argued for first metatarsal and distal phalangeal characters). The series of tarsal groups found in the Shanghuang fissure fillings gives strong support to the view that primitive anthropoidean-like postcranial features are retained from a primitive primate ancestor. And in fact, the discovery of an anthropoidean-like calcaneum in the Earliest Eocene *Archicebus* provides an even more striking confirmation (Ni et al. 2013). A full understanding of the locomotor adaptation of the earliest primates will require further study and more fossils. At present, the postcranial evidence for eosimiids is roughly that of primitive primates, which does not prove their anthropoidean affinities.

The Asiatic connection rooting African simiiforms in the Asiatic eosimiids is essentially based on parsimony analyses of large datasets (e.g., Marivaux et al. 2005; Beard et al. 2009; Seiffert et al. 2005a, b, 2010b; Ni et al. 2013; Fig. 36). As mentioned above concerning amphipithecids, these analyses can be misled by convergences due to similar selective forces (e.g., bunodonty linked with similar frugivory and/or hard food requirements). They also suffer recurrent difficulties concerning the independence of characters, their weighting, missing data, etc. The number of characters and taxa will never replace the absence of intermediates or make up for uncertainties due to the lack of what would be the most diagnostic characters. An example in primate phylogeny was given by Marivaux et al. (2001), in which a global parsimony analysis nested *Bugtilemur* within living cheirogaleids when this fossil lacked a real tooth comb. It thus could not be a lemuriform. Linked to the discovery of a related and more complete genus, *Bugtilemur* was subsequently recognized as a probable adapiform (Marivaux et al. 2006). In this case, the many similarities with cheirogaleid jugal dentition overweighted the phylogenetic signal issued from the tooth comb. A high number of convergences in dental details can obscure the true phylogenetic relationships. Such will be the case for all the large data sets used to uncover primate phylogeny as long as several fossil groups lack key phylogenetic information, and at the same time are separated by large gaps in the fossil record, preventing the recovery of enough intermediates in other suites of characters. It is worth noting here that such analyses can also generate trees which imply as many as six dispersals of stem anthropoideans between continents (Ni et al. 2013), which appears historically unrealistic. A morphologically parsimonious tree can be historically unlikely or even impossible.

Among the reasons to doubt an Asiatic origin of simians is lack of historical likelihood. Anthropoideans are a well-adapted, successful group in Africa and

South America, including the Caribbean islands. If they had been present in Asia, why didn't they leave some group of successful survivors behind there? Asiatic forests are the refuge of many primitive mammals, many tree shrews, and *Tarsius* found refuge in islands; they were the refuge of adapiforms until the Late Miocene, until the spread of African monkeys. Would they have been the place of the first radiation of anthropoideans without leaving any Asiatic descendants? Such a scenario seems very unlikely. If there had been a radiation of Eocene-Oligocene anthropoideans in Asia, successful enough to colonize Africa through one or multiple dispersals, they would have left descendants in Asia too, alongside the cohort of primitive Asiatic mammals. The extinction of all early Asiatic anthropoideans would be a very unlikely historical event – incongruous with the remarkable ability of all kinds of groups, including primates, to survive over long periods of time. That argument is not definitive, of course, because the past is also full of surprises. However, paleontologists should pursue a coherent account of history as much as, if not more so than, a parsimonious distribution of morphological characters considered in isolation from the geological and geographic context of the fossils to which they belong. The argument of historical likelihood, added to the lack for now of convincing evidence, should lead us to consider favorably the third scenario – that of an ancient differentiation in Africa (Fig. 36).

Afrotarsiidae

The enigmatic genus *Afrotarsius* is gaining great importance in connection with the scenarios laid out above. *A. chatrathi* is known through one mandible bearing M/1–M/3 and parts of the base of the crown of P/4 and P/3. Its molars with high pointed cusps and its trigonids with paraconid similar from M/1 to M/3 are close to those of *Tarsius*, and it was initially described as a tarsiid (Simons and Bown 1985). Unsurprisingly, some large parsimony analyses place it close to *Tarsius* (Seiffert et al. 2005a). It differs from *Tarsius* by several characters, including an M/1 larger than M/2–3 and M/3 without an elongated third lobe. Possible ties with early anthropoideans were also found (Fleagle and Kay 1987; Kay and Williams 1994), and similarities with eosimiids were noted (Ross et al. 1998; Godinot 2010). New material attributed to the new species *A. libycus* includes two upper molars and two P3/, an important addition (Jaeger et al. 2010). These teeth add to the similarities with eosimiids; however, the upper molars also show the postmetaconule-crista directly linked to the posterolabial corner of the tooth, a very primitive character which must have been retained from an ancestor more primitive than eosimiids, leading to use of the family Afrotarsiidae proposed earlier (Jaeger et al. 2010). The P3/ are very small and their labially deflected postparacrista suggests a marked insectivorous specialization.

Another putative afrotarsiid, *Afrasia djidjidae*, was recently described from the Pondaung Formation of Myanmar (Chaimanee et al. 2012). This species is known by four isolated teeth only, coming from three different localities. The type M2/ is very similar to that of *Afrotarsius libycus*, but there are some differences, and several characters of the other teeth are more reminiscent of eosimiids. The placement of *A. djidjidae* in afrotarsiids is tentative, and is associated with a cladogram showing several evidently incorrect parts (*Teilhardina* as a terminal branch of Omomyidae + Tarsiidae). The authors conclude that an afrotarsiid dispersal took place between Asia and Africa shortly before these Middle Eocene localities. Such a conclusion is hasty. Characters linked to an insectivorous specialization are difficult to disentangle from primitive characters. Much more material will be needed to understand the differences between eosimiids (*Eosimias* with long P/3 and P/4) and afrotarsiids (*Afrotarsius* with broad and short P/4). What will *Afrasia* be? The real afrotarsiids might equally well have issued from a much earlier dispersal, which would have given birth to a new adaptive radiation of stem simians or simians. This would increase and broaden the spectrum of adaptations in the two parallel radiations of African simiiforms + stem simiiforms, and Asiatic tarsiiforms. Earlier and more complete fossils are needed to clarify these hypotheses.

Further Important Phylogenetic Questions, and a Provisional Conclusion

A number of important issues are associated with the understanding of fragmentary fossils. Such finds are tantalizing, because the implications of their analysis might be far-reaching; but they are also frustrating, because the associated discussion is very technical and the results are bound to remain tentative, due to such specimens' incompleteness or isolation from other, better understood fossils. First in the list is *Altiatlasius koulchii*, from the Late Paleocene Adrar Mgorn locality in Morocco. As the only Paleocene primate known to date, it is very important. Yet it is documented only by eight isolated teeth. The upper molars show extremely primitive characters (stylar shelf), but also some characters – such as a slight bunodonty and a continuous lingual cingulum on M2/ – which would make it derived in comparison with *Donrussellia* and *Teilhardina*, and possibly a sister group of the African simian radiation (Sigé et al. 1990; Godinot 1994). A recent phylogenetic analysis, based on a very large data set, positions *Altiatlasius* as the earliest member of the stem anthropoideans (Ni et al. 2013). Such far-reaching conclusion needs to be strengthened by more complete fossil evidence, especially since some early African strepsirhines appear to have been very bunodont (Tabuce et al. 2009). Yet this unique fossil is an important signal, because it might indeed document stem haplorhines or stem anthropoideans.

Two fossils from the Middle Eocene of Namibia are the first Eocene primates named from Sub-Saharan Africa. They are a maxilla with M2/ and M3/, which is the type of *Namaia bogenfelsi* (Pickford et al. 2008), and a smaller P/4, which is also referred to it. The upper maxilla belongs to a primitive primate that has overall similarity with European anchomomyin adapiforms, but also significant differences. Its lingual half is anteroposteriorly more reduced than in anchomomyins, and it bears a well-formed cuspidate metaconule, such as is never seen in anchomomyins and extremely rare in adapiforms. The P/4 is unlike that of any adapiform and might suggest simian affinities, although it has a smaller size than the maxilla and could pertain to a different taxon. More material is needed to determine the number and the affinities of the primates present in this locality.

Finally, to give a last example, the enigmatic *Nosmips* was described from the BQ-2 locality of the Fayum, Egypt (earliest Late Eocene). Its surprising characters led to the name *N. aenigmaticus* (Seiffert et al. 2010b). Its lower molars have lost their paraconids, but their trigonids nevertheless increase in length from M/3 to M/1. Inasmuch as their trigonids are much higher than their talonids, they are more reminiscent of the lower molars of prosimians than of simians; however, the anteroposterior cristid obliqua and the short M/3 talonid look simian-like (primitive?). One upper molar appears very simple, with an incomplete lingual cingulum and no hypocone. A posterior waisting gives it a primitive stamp. This species is specialized through its premolars, with both P3/ and P/3 anteroposteriorly long and high. The lower P/3 has a voluminous metaconid and an anteriorly extended and curved protocristid, which presumably had a honing function with a large upper canine. The P/4 is lower, more molarized, and morphologically intermediate with the lower molars. Parsimony analyses of 361 morphological characters give, depending on different assumptions, very different results: stem anthropoidean, stem lemuriform, or adapiform status (Seiffert et al. 2010b). This example once more demonstrates the unability of such large analyses to uncover a good phylogenetic signal in the presence of overlapping dental similarities with species belonging to different infraorders. Lower molar morphology, as well as long, highly molarized, and specialized P/3–4 are more suggestive of stem lemuriform affinities, which represent the most rational assumption. However, other affinities are also possible. In any case, this genus reveals one more ancient lineage in Africa, which, along with the genera cited above, highlights the fact that our knowledge of early African fossil primates remains very incomplete.

To conclude our discussion of primate phylogeny: the last decade has witnessed a number of surprising discoveries, which show that our knowledge of the Paleogene primate fossil record is still only very partial. The European and North American radiations are relatively well circumscribed, with only a few open questions for now: Where does *Rooneyia* come from? Where do the adapines come from? The African and Asiatic records are much less completely known and have been the subject of the greatest surprises: *Afradapis*, an adapiform convergent with catarrhines in its anterior dentition; the azibiids, tiny strepsirhines with upper molars convergent on bunodont simians; *Bugtilemur*, an adapiform convergent with living cheirogaleids; *Nosmips*, an enigmatic form for which there is hesitation between strepsirhine and simian! All of these findings call for caution concerning the interpretation of dental characters for fragmentary fossils pertaining to distantly related groups. Nevertheless, great advances have been made. Among them, the discovery of Eocene lemuriforms and stem lemuriforms in Africa is decisive for our understanding of the origin of this living infraorder. It supersedes all previous, speculative efforts to root these groups near different genera of adapiforms. The discovery of *Teilhardina asiatica* shows that intercontinental dispersals can be precisely followed also from Asia to other continents (this should be possible for the putative anthropoidean ancestors as well, then!).

A broad and monophyletic Asiatic family of amphipithecids is also a step forward, even if their origin and phylogenetic place remain controversial. *Archicebus* bears directly on concepts of the earliest primate diversification. A complete fossil, such as the skeleton of *Darwinius masillae*, should produce further information on rarely found parts of the primate skeleton. Ongoing functional and phylogenetic study of hands and feet, tarsals, and phalanges should continue to contribute significantly to the understanding of primate phylogeny. This field is very active, and still has a lot to discover.

Conclusion: Evolution in Paleogene Primates

The fossiliferous part of the Paleogene, Eocene plus Oligocene, spans roughly 30 My. Over the course of this time interval, it is possible to observe major steps in primate evolution. These steps can best be studied in the regions where the fossil record is the richest, the North American and the European Eocene, even if the fossil groups found there became extinct without leaving descendants among the living groups. The well-known Eocene radiations started with the arrival of one genus each, e.g., *Teilhardina*, *Cantius*, or *Donrussellia*. From this genus a diversification took place, accompanied by increases in size in some of the lineages. When the record is dense enough, dental morphology allows an almost direct reading of lineages. More often the record is not as good as that, but the relevant evolutionary trends are so general that reading the polarity of dental traits is usually straightforward. Only the large number of convergences can obscure the reconstruction of phylogeny, as seen for example in omomyines. These dental trends raise interesting questions. Why does the paraconid become reduced? And, why does a hypocone develop at the same place in so many different lineages? Hypocones occur at roughly the same size, suggesting the existence of a developmental constraint, which it would be important to understand. Incidentally, this question brings up the difficult issue of character coding: should characters that we know not to be homologous be coded in the same way? For example, the hypocone in omomyines is not homologous with that of microchoerids, and the latter is not homologous with the hypocones which develop in several lineages of adapiforms, etc. This information is most often ignored in cladistic analyses. Reduction of some antemolar teeth is also a common trend, which is sometimes related to a size increase in the anterior incisor and “compression” of teeth between it and P/4, but at other times occurs without evident dental specialization and is then probably related to muzzle shortening.

Changes in molar morphology are related to changes in diet, and diet is highly correlated with size. Small species weighing below 500 g are usually predominantly insectivorous, whereas species above 500 g become more frugivorous or folivorous (Kay 1975). There are many mixed feeders among living and fossil primates, and most often their protein intake comes from insects for the small species, and from leaves for the large ones. The broad picture is that the Late Paleocene–Earliest Eocene primates were mainly insectivorous and more or less mixed feeders, with *Cantius* already quite frugivorous. By the end of the Early Eocene, some larger species had evolved more specialized dentitions. For example, *Notharctus* had acquired molars with increased shearing crests, forming the labial W on upper molars that we see in living folivores. By the Middle and Late Eocene, other genera, such as *Caenopithecus* and *Afradapis*, had developed similar morphologies, and lower molar shearing crests had strongly increased in the adapines. More bunodont dentitions evolved many times. Extreme degrees of bunodonty, adapted to frugivory and/or the processing of hard food, developed in Asiatic amphipithecids and in African parapithecids and propliopithecids. Some fossils developed dental specializations unknown in living primates. *Necrolemur, Microchoerus*, the tarkadectines, and other genera developed highly crenulated teeth, probably adapted to some kind of resistant food. The very small azibiids are astonishing: how could such tiny species have become so extremely bunodont? Paleogene primates broaden the spectrum of dental and dietary adaptations of the order.

Alongside the Paleogene primate diversifications, locomotor adaptations evolved as well. Quite a number of the Early Eocene prosimians are reconstructed as “cheirogaleid-like” –which indicates a mixture of quadrupedalism, climbing, and leaping. However, there is debate about the ancestral morphotype of locomotor adaptation, with or without much leaping (as mentioned above in the anthropoidean origin part). In some groups, it seems that locomotion changed essentially through a more or less marked increase in leaping propensities (weak in omomyids, more pronounced in the larger notharctines). It has recently been suggested that some tarsal lengthening might be a compensatory effect in grasping foot postures, and not an indication of leaping propensities (Moyà-Solà et al. 2012). This hypothesis needs to be closely examined. Only during the Middle and Late Eocene did one lineage, the *Necrolemur–Microchoerus* group, increase its leaping specialization to a degree similar to the living VCL, which move through the forest by long leaps and adopt vertically clinging postures at rest. However, we know that very different adaptations developed in some other groups. Quadrupedalism and climbing (slow climbing?) are present in amphipithecids and adapids. The Late Eocene–Oligocene anthropoideans also show quadrupedalism and climbing, with more leaping propensities in parapithecids. A variety of adaptations developed among European adapines, including different degrees of quadrupedalism and climbing. To date, there is no clear evidence of ateline-like forelimb suspension in Paleogene primates.

Important aspects of the evolution of sense organs and the brain can be traced as well in Paleogene primates. Most characteristic since their origin are the large eyes of primates. It has been known for a long time that nocturnal primates can be distinguished from diurnal ones by their possession of relatively larger eyes, as mentioned above for many fossil groups. A deeper understanding of visual evolution became possible once size measurements of the optic foramen were used to infer the degree of retinal summation and visual acuity in fossils (Kay and Kirk 2000). Visual characteristics are typically shared by large groups; however, fossils also reveal multiple changes. Most omomyiforms are reconstructed as nocturnal, yet *Teilhardina asiatica* was found to have small orbits, like diurnal species. Among cercamoniines, *Europolemur* was found to have small orbits, like diurnal forms (such as the adapines and *Notharctus*); however, *Pronycticebus* and *Darwinius* had orbits indicating nocturnal habits. The anthropoidean *Biretia megalopsis* exhibits nocturnal-sized orbits as well. All of these examples reveal that important behavioral shifts took place in the Eocene. There will be more to learn about this crucial aspect of primate behavior. *Adapis* is found to have a strangely high degree of retinal summation. Why? No adapiform or omomyiform studied by Kay and Kirk (2000) showed optic foramen dimensions as large as those in extant diurnal anthropoideans, whose visual acuity (inferred for diurnal ancestral haplorhines because *Tarsius* has a fovea) is extremely high. Finding intermediate values in some fossils would be crucial.

The use of CT-scan techniques allows access to quantitative parameters of the bony labyrinth. Two kinds of sensory capacities can be extracted. Cochlear labyrinth volume is correlated with hearing abilities (Kirk and Gosselin-Ildari 2009). Ongoing studies have already yielded results. For instance, assessments of high and low frequency limits of hearing show that *Necrolemur antiquus* had better high frequency hearing than three other fossils, similar to that of the living *Galago senegalensis*, whereas *Adapis* had capacities similar to those of the living *Perodicticus* (Ludeman et al. 2013). The size and morphology of the semi-circular canals also give interesting information. The first studies interpreted relative semi-circular canal size, estimated via the radius of curvature, to correlate directly with relative degrees of agility among species (Spoor et al. 2007; Silcox et al. 2009). This way, adapines were found to be less agile than *Smilodectes* and *Notharctus*, and *Microchoerus* faster and more agile than the latter, which was in line with the modes of locomotion of these taxa as reconstructed from postcranials. However, further studies have put these results in question, because it appears that it is the orthogonality of the semi-circular canals, more so than their radius of curvature, that is related to the speed of head movements (Malinzak et al. 2012).

The size of the infraorbital foramen is highly correlated with the size of the infraorbital nerve, which transmits signals from the mechanoreceptors of the orofacial region. It had been assumed that the infraorbital foramen, which is smaller in primates than in most non-primate mammals, was larger in strepsirhines than in haplorhines (Kay and Cartmill 1977). This size difference within mammals was interpreted to roughly correlate with vibrissae number, and was used in this way in several studies to support a haplorhine status for fossils showing a relatively small infraorbital foramen (e.g., Beard and Wang 2004), or conversely, to infer a strepsirhine and probably nocturnal habit for others (e.g., Tabuce et al. 2009). However, a much larger study of primates and other mammals has failed to confirm such differences in terms of vibrissae counts. Haplorhines and strepsirhines appear not to differ in infraorbital foramen area, nor in macrovibrissae counts, but to differ in microvibrissae counts – and in the opposite direction from what was expected: it is haplorhines that have more (Muchlinski 2010a). Information about the mechanoreceptors of the oral region can be gained from the relative size of the infraorbital foramen; however, for now the implications appear to be primarily ecological, with frugivores having larger foramina and more vibrissae than insectivorous and folivorous primates (Muchlinski 2010b). This approach already fits better with the relatively small infraorbital foramen found in *Adapis* (Gingerich and Martin 1981).

Important aspects of brain evolution in primates are obtained through the study of endocranial casts. The latter provide not only quantitative information – that is, absolute brain measurements – but also qualitative information, because most neocortical sulci delimit functional or somatotopic areas. If these sulci can be confidently homologized, behavioral and sensory specializations can be inferred. The oldest primate endocast is that of Early Eocene *Tetonius homunculus*, known since its preliminary description by Cope. Taking into account the modest deformation of the skull, Radinsky (1967) proposed a reconstruction with a width–length index of 1.07. He noted that the frontal lobes were smaller relative to the rest of the cerebrum than in any extant primate. Only a shallow Sylvian fissure can be recognized, but this is not an indication of primitiveness because similar-sized living prosimians have similarly smooth brains. The olfactory bulbs of *Tetonius* are relatively larger than in any living primate. As noted by Radinsky, these primitive characters notwithstanding, compared to contemporaneous ungulates *Tetonius* had a very advanced brain with enlarged temporal and occipital lobes and reduced olfactory bulbs. A natural endocast of the Middle Eocene *Smilodectes gracilis* was described in detail and beautifully illustrated by Gazin (1965). It is also very smooth, shows only a shallow sulcus lateralis not far from the midline of the brain, and, surprisingly, does not feature a recognizable Sylvian sulcus. Gazin noted the extended neopallium, which is relatively greater than in any other Middle Eocene mammal for which such information is available. He also noted a close similarity with the brain of extant *Eulemur*, insofar as the cerebellum is not overlapped by the cerebrum. The cerebellum of *Smilodectes* is short and narrow in comparison with its width, and the vermis and lateral lobes are prominently developed. Both *Tetonius* and *Smilodectes*, an Early and a Middle Eocene primate, show expanded temporal and occipital areas, suggesting well-developed acoustic and auditory capacities, respectively. Gazin (1965) rightly correlated the enlarged visual cortex area with the large, forward-facing orbits of *Smilodectes*. Recent analyses show that binocular vision is correlated with the expansion of visual brain structures, and consequently with expansion of overall brain size, in primates (Barton 2004). More generally, advances in visual capacities have been correlated with increases in brain size in primate evolution (Kirk 2006).

The endocast of the Late Eocene *Adapis* was the first to be described (Neumayer 1906) and has been mentioned many times by many authors. A better preserved endocast was described by Gingerich and Martin (1981). Both endocasts exhibit a true Sylvian sulcus, a universal trait in extant primates but lacking in *Smilodectes*. Among other possible differences between notharctine and adapine brains are the large and pedunculate olfactory bulbs in *Adapis*, relative to which those of *Smilodectes* are small (Radinsky 1970). This distinction aside, both appear primitive in comparison with living primates. Attempts to quantify encephalization through a quotient relating brain size to body size have led to some controversy, mainly due to difficulties in estimating body size, i.e., body weight, in fossil primates (Radinsky 1977; Jerison 1979). In any case, there is consensus that both *Adapis* and *Smilodectes* had smaller brains in relation to body size than do living strepsirhines. On the other hand, the Late Eocene *Necrolemur* and the younger *Rooneyia* are found to have encephalization levels similar to those of living prosimians. The endocast of the Early Oligocene *Aegyptopithecus* was mentioned above. It shows a central sulcus as in living anthropoideans, and appears advanced over strepsirhines in having relatively more visual cortex and smaller olfactory bulbs. However, in quantitative terms it is smaller than in any living anthropoidean, having an encephalization level similar to some prosimians or even below (Radinsky 1973; Simons 1993; Simons et al. 2007). The endocast of *Parapithecus (Simonsius) grangeri* has been extracted by CT-scanning techniques (Bush et al. 2004). It also appears smaller relative to body size than in living anthropoideans. Its olfactory bulbs are at the lower limit of those of strepsirhines.

A last source of information relating to behavior is provided by sexual dimorphism, which was long suspected in *Notharctus* (Gregory 1920; Gingerich 1979) and convincingly shown in one assemblage of *N. venticolus* (Krishtalka et al. 1990). Evidenced through canine size and shape, it was shown subsequently to affect skull shape in *N. tenebrosus* and *Smilodectes gracilis* (Alexander 1994; Alexander and Burger 2001). Sexual dimorphism is suspected in *Cantius torresi* based on the size difference between two canines, and size differences in mandibular depths in six specimens (Gingerich 1995). It thus seems to be a characteristic of notharctines. Its presence in adapines is unknown, due to the lack of homogeneous assemblages (the only available one, for the large *Magnadapis* from Euzet, does not present any dimorphism; Gingerich 1977b). A marked sexual dimorphism has been found, however, in the latest Eocene adapid *Aframonius* (Simons et al. 1995). An extremely high dimorphism, including body size dimorphism, is found in propliopithecids. The conclusion that a marked sexual dimorphism is also found in the smaller *Proteopithecus* and *Catopithecus* modified the view, based on observations in living primates, that sexual dimorphism is highly correlated with body size. It appears to be a characteristic of simiiforms, acquired early and probably linked to their diurnal habits (Simons et al. 1999). Sexual dimorphism is an indication of distinctive social structures, usually interpreted as indicating life in polygynous groups, high male-male competition when it is pronounced, and single male dominance when it is highly pronounced. However, this is a complex question; precise social structures cannot be inferred, especially for low levels of dimorphism. What is important is that social evolution along these lines also happened in some adapiforms in the Early Eocene, and was advanced in Late Eocene anthropoideans. Social life is an important predictor of increased brain size, which is believed to have played a major role in later simian brain evolution. In sum, not only was binocularity present in the earliest primates; higher visual acuity and social factors as well were already present in Paleogene primates, enabling later brain developments.

When the fossil record is good, each primate species can be studied for its adaptations, and faunistic aspects can also be analyzed. In the big picture, primate radiations are constrained by climatic and biogeographic factors, as laid out in the Introduction to this chapter. Within these radiations, interesting primate faunal successions are known, which are more or less understood. For example, the replacement of cercamoniines by adapines in Europe around MP13–MP14 (Figure 7) is due to a dispersal. But why did mid-sized or large cercamoniines disappear? Were the more folivorous adapids better adapted to changing environments? In the Late Eocene of Africa, in the Fayum, adapids were the large-sized primates, whereas anthropoideans and lemuriforms of the same localities were smaller. Adapids disappeared by the end of the Eocene, and anthropoideans became progressively larger during the Early Oligocene. Were these developments also related to environmental changes? A much better-studied example, made possible by a more extensive geological and paleontological record, is the Early–Middle Eocene transition in several of the Rocky Mountain basins of Wyoming and adjacent states, from anaptomorphine dominance in the Wasatchian to omomyine dominance in the Bridgerian. Furthermore, the diversification of the omomyines in the Bridgerian is striking. This raises two interesting issues. First, continued research in basin margin areas (southwestern Bighorn Basin, northeastern edge of the Green River Basin), has led to the realization that anaptomorphines remain in fact relatively diverse in these marginal areas (e.g., Bown 1979; Muldoon and Gunnell 2002). The shift from anaptomorphine to omomyine dominance in lowland habitats probably was an ecological replacement, with anaptomorphines being pushed toward upland refugia when omomyines had found favorable habitats and reached dominance in basin areas. The second issue relates to the rapid diversification of the omomyines: did basin margins provide heterogeneous habitats favorable to the rise of evolutionary innovations? Answering such a question requires detailed paleoenvironmental studies. What is remarkable in the Rocky Mountain Eocene record is that it provides, in the Bighorn and in other basins, some of the best examples of detailed lineages – phylogeny followed through time as close as one can get, and also, at a more regional scale, fine-grained aspects of replacements, refugia, and their possible role in evolution. In such locations, the study of fossil primates can contribute to the detailed elucidation of the mechanisms of evolution.

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Fossil Record of Miocene Hominoids

David R. Begun

Contents

D.R. Begun (✉)
Department of Anthropology, University of Toronto, Toronto, ON, Canada
e-mail: begun@chass.utoronto.ca

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Abstract

Hominoids, or taxa identified as hominoids, are known from much of Africa, Asia, and Europe since the Late Oligocene. The earliest such taxa, from Africa, resemble extant hominoids but share with them mainly primitive characters. Middle and Late Miocene taxa are clearly hominoids, and by the end of the Middle Miocene, most can be attributed to either the pongine (*Pongo*) or hominine (African ape and human) clade. Interestingly, there is no definitive fossil record of the hylobatid clade (gibbons and siamangs), though there have been some proposed candidates. Miocene hominoids experienced a series of dispersals among Africa, Europe, and Asia that mirror those experienced by many other contemporaneous land mammals. These intercontinental movements were made possible by the appearance of land bridges, changes in regional and global climatic conditions, and evolutionary innovations. Most of the attributes that define the hominids evolved in the expansive subtropical zone that was much of Eurasia. Hominines and pongines diverge from each other in Eurasia, and the final Miocene dispersal brings the hominine clade to Africa and the pongine clade to Southeast Asia. Having moved south with the retreating subtropics, hominines and pongines finally diverge in situ into their individual extant lineages.

Introduction

Nonhuman fossil hominoids represent a highly diverse and successful radiation of catarrhine primates known from many localities ranging geographically from Namibia in the south, Germany in the north, Spain in the west, and Thailand in the east, and temporally from Oligocene deposits in Kenya to the Pleistocene of China (Fig. 1). More than 50 genera of nonhuman hominoids are known (Table 1), probably a small percentage of the total number that have existed. Given the focus of these volumes on ape and especially human evolution, this survey of the fossil record of Miocene hominoids will concentrate on taxa that most or all researchers agree are hominoid and in particular on taxa that are most informative on the pattern and biogeography of modern hominoid origins.

What Is a Hominoid?

Most of the fossil taxa attributed to the Hominoidea or the Hominidea (new rank, Table 2) in this chapter are known to share derived characters with living hominoids. Because the two living families of the Hominoidea, Hylobatidae and Hominidae, share characters that are either absent or ambiguous in their development in *Proconsul* and other Early Miocene taxa, a new rank is proposed here to express the monophyly of the Hominoidea and the monophyly of catarrhines more closely related to extant hominoids than to any other catarrhine. The magnafamily Hominidea (a rank proposed in a work on perissodactyl evolution; Schoch 1986)

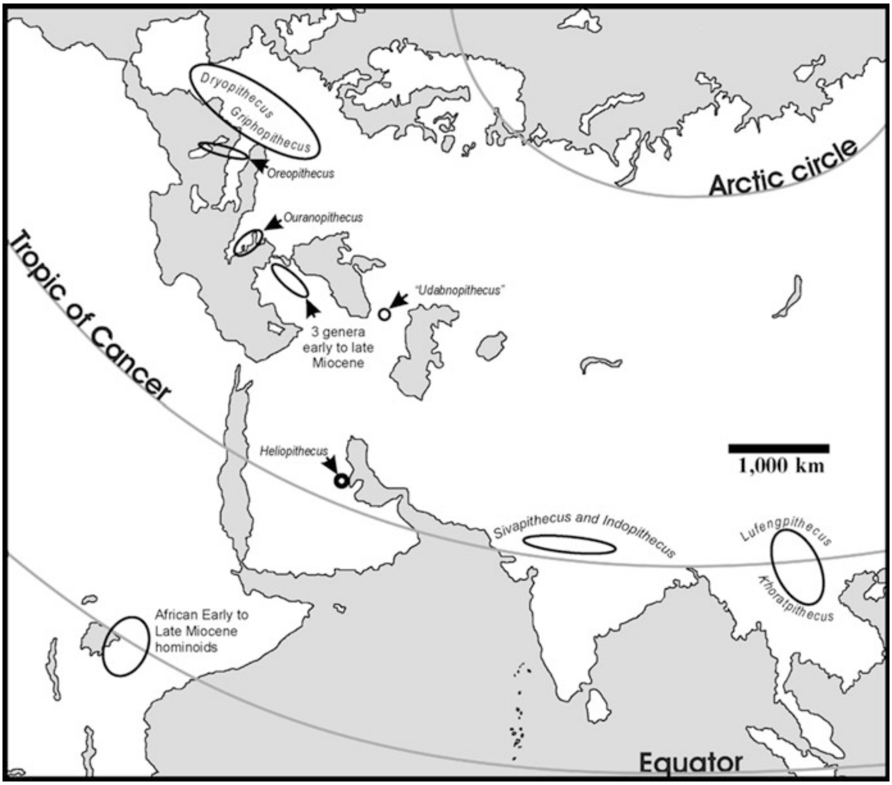

Fig. 1 *Map* showing the location of the Miocene taxa discussed in this chapter. Namibia (southern Africa), from which *Otavipithecus* was recovered, is not shown

unites Proconsuloidea with Hominoidea to the exclusion of other catarrhines. This differs from Harrison's use of the term proconsuloid that he sees as referring to the sister taxon to cercopithecoids and hominoids (Harrison 2002).

A few taxa are included in this review if they are too poorly known to preserve unambiguous hominoid synapomorphies but closely resemble other better-known fossil hominoids. In general, fossil and living hominoids retain a primitive catarrhine dental morphology. This makes it difficult to assign many fossil taxa to the Hominoidea since a large number are known only from teeth and small portions of jaws. Dentally, the most primitive Hominidea differ only subtly from extinct primitive catarrhines (propliopithecoids and pliopithecoids) (Fig. 2, node 1). Propliopithecoids (*Propliopithecus*, *Aegyptopithecus*) are usually smaller and have much more strongly developed molar cingula, higher cusped premolars, and smaller incisors and canines (Begun et al. 1997; Rasmussen 2002; see chapter "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3). Pliopithecoids (*Pliopithecus*, *Anapithecus*) are also generally smaller and have molars with more strongly expressed cingula, more mesial protoconids, and relatively small anterior teeth (Begun 2002). However, the differences between Late Miocene hominids and

Table 1 Genera of fossil ape or apelike taxa[a]

	Age	Ma	Genera	Important localities	Country	Material[b]
1	Oligo.	28–29	*Saadanius*	Harrat Al Ujayfa	Saudi Arabia	Facial cranium
2	Oligo.	25.2	*Rukwapithecus*	Rukwa Rift	Tanzania	Mandibular fragment
3	Oligo.	25	*Kamoyapithecus*[c]	Lothidok	Kenya	Craniodental fragments
4	e M	21	"Proconsul meswae"[d]	Meswa Bridge	Kenya	Craniodental fragments
5	e M	?20–17.5	*Morotopithecus*	Moroto	Uganda	Cranial, dental, postcrania
6	e M	?20–17.5	*Kogolepithecus*[c]	Moroto	Uganda	Dental
7	e M	19	*Ugandapithecus*[d]	Napak/Songhor	K/U	Cranial, dental, postcrania
8	e M	19	*Xenopithecus*[c]	Koru	Kenya	Craniodental fragments
9	e M	19	*Proconsul*	Songhor/Koru	Kenya	Cranial, dental, postcrania
10	e M	19	*Limnopithecus*[c]	Koru/Songhor	Kenya	Craniodental
11	e M	19	*Rangwapithecus*[c]	Songhor	Kenya	Craniodental
12	e M	19	*Micropithecus*[c]	Napak/Koru	K/U	Craniodental
13	e M	19	*Kalepithecus*[c]	Songhor/Koru	Kenya	Craniodental fragments
14	e M	18–19	*Dendropithecus*[c]	Rusinga/Songhor/Napak/Koru	K/U	Cranial, dental, postcrania
15	e M	19	*Lomorupithecus*	Napak	Uganda	Craniodental fragments
16	e M	19.5–17	cf. *Proconsul*[e]	Rusinga/Mfangano	Kenya	(Cranial, dental, postcrania)+
17	e M	17.5	*Turkanapithecus*	Kalodirr	Kenya	Cranial, dental, postcrania
18	e M	17.5	*Afropithecus*	Kalodirr	Kenya	Cranial, dental, postcrania
19	e-m M	17.5–15	*Simiolus*	Kalodirr/Maboko	Kenya	Cranial, dental, postcrania
20	e-m M	17.5–15	*Nyanzapithecus*	Rusinga/Maboko	Kenya	Craniodental fragments
21	e M	17	*Heliopithecus*	Ad Dabtiyah	S. Arabia	Dental

22	e M	16.5	cf. *Griphopithecus*	Engelswies	Germany	Dental
23	e M	16	*Griphopithecus*	Paşalar/Çandır	Turkey	Cranial (dental)+, postcrania
24	m M	15	*Equatorius*	Maboko/Kipsarimon	Kenya	(Cranial, dental, postcrania)+
25	m M	15	*Mabokopithecus*	Maboko	Kenya	Dental
26	m M	15	*Nacholapithecus*	Nachola	Kenya	Partial skeleton
27	m M	13	*Kenyapithecus*	Fort Ternan	Kenya	Cranial, dental, postcrania
28	m M	13	*Otavipithecus*	Otavi	Namibia	Craniodental, vertebra
29	m M	12.5	*Pierolapithecus*	Els Hostalets de Pierola	Spain	Partial skeleton
30	m M	12.5	*Dryopithecus*	St. Gaudens, La Grive	France	Mandibles + teeth
31	m M	12.5	*Anoiapithecus*	Els Hostalets de Pierola	Spain	Craniodental
32	m-l M	12.5–7	*Sivapithecus*	Potwar Plateau	Pakistan	(Cranial, dental, postcrania)+
33	m-l M	?13.5–7	*Khoratpithecus*[f]	Magaway (M), Khorat)/Ban Sa (Th.)	Thailand/Myanmar	Craniodental fragments
34	l M	10	*Rudapithecus*	Rudabánya	Hungary	(Cranial, dental, postcrania)+
35	l M	10–9	*Hispanopithecus*	Can Llobateres/Can Ponsic	Spain	(Cranial, dental, postcrania)+
36	l M	11–8?	*Neopithecus*[g]	Salmendingen	Germany	m3
37	l M	10	*Ankarapithecus*	Sinap	Turkey	Cranial, dental, postcrania
38	l M	9.5	*Samburupithecus*	Samburu	Kenya	Craniodental fragments
39	l M	10.25	*Chororapithecus*	Chorora Fm	Ethiopia	Isolated teeth
40	l M	9.85	*Nakalipithecus*	Nakali	Kenya	Mandible and teeth
41	l M	9.5	*Ouranopithecus*	Ravin de la Pluie	Greece	(Craniodental)+, 2 phalanges
42	l M	9–8	*Graecopithecus*	Pygros	Greece	Mandible
43	l M	9–8	*Lufengpithecus*	Lufeng	China	(Cranial, dental)+, postcrania

(*continued*)

Table 1 (continued)

	Age	Ma	Genera	Important localities	Country	Material[b]
44	l M	8–7	New taxon	Çorakyerler	Turkey	Mandible, maxilla
45	l M	7	*Oreopithecus*	Baccinello/Monte Bamboli	Italy	(Cranial, dental, postcrania)+
46	l M	7–6	*Sahelanthropus*	Toros-Menalla	Chad	Craniodental
47	l M	6.5	*Indopithecus*	Potwar Plateau	Pakistan	Mandible
48	l M	6	*Orrorin*	Lukeino	Kenya	Craniodental, postcrania
49	l M	5.8–5.2	"*Ardipithecus*"[h]	Alayla (Middle Awash)	Ethiopia	Craniodental, postcrania
50	Pl.	1–0.3	*Gigantopithecus*	Liucheng	East Asia	Mandibles, teeth

Oligo. Oligocene, *e M* Early Miocene, *e-m M* early Middle Miocene, *m M* Middle Miocene, *m-l M* Middle-Late Miocene, *l M* Late Miocene, *K*/*U* Kenya and Uganda, *Pl.* Pleistocene, *M* Myanmar (Burma), *Th.* Thailand

[a] These 50 genera include taxa from the Oligocene and Early Miocene that share mainly primitive characters with the Hominoidea but that appear to be derived relative to pliopithecoids and propliopithecoids. Please see text for further discussion

[b] Material briefly described by part representation. Dental = mainly isolated teeth; Dental, mandible, maxilla = known only from these parts; Craniodental fragments = teeth and few cranial fragments; Craniodental = larger samples of more informative cranial material; Cranial, dental, postcrania = good samples from each region; ( ) + = very good representation of parts in parentheses

[c] Unclear attribution to Hominoidea

[d] Large taxon possibly distinct from *Proconsul*

[e] *Proconsul* from the Rusinga and Mfangano localities in Kenya is likely to be distinct at the genus level from the *Proconsul* type material

[f] Middle Miocene samples attributed to this taxon are more fragmentary and may not be congeneric

[g] The *Neopithecus brancoi* type is an isolated M_3 that some attribute to the Pliopithecoidea while other to *Dryopithecus* (Begun and Kordos 1993). I regard this as a nomen dubium

[h] "*Ardipithecus kadabba*." The type of the genus, *Ardipithecus ramidus*, is younger and shares derived characters with australopithecines not present in *A. kadabba*, making *Ardipithecus* in my opinion paraphyletic

Table 2 A taxonomy of the Hominidea

Cercopithecidea (Magnafamily, new rank)	
Hominidea (Magnafamily, new rank)	
Proconsuloidae	Crown hominoids of uncertain status
Proconsul	*Kenyapithecus*
cf. *Proconsul*	*Oreopithecus*
Samburupithecus	Family incertae sedis
Micropithecus	*Afropithecus*
Hominoidea	*Morotopithecus*
Hylobatidae	*Heliopithecus*
Hylobates	*Griphopithecus*
Hominidae	*Equatorius*
	Nacholapithecus
Dryopithecus[a]	*Otavipithecus*
Hispanopithecus	
Rudapithecus	
Ouranopithecus	Superfamily incertae sedis
Graecopithecus	*Rangwapithecus*
Sivapithecus	*Nyanzapithecus*
Lufengpithecus	*Mabokopithecus*
Khoratpithecus	*Turkanapithecus*
Ankarapithecus	Magnafamily incertae sedis
Gigantopithecus	*Kamoyapithecus*
Indopithecus	
Chororapithecus	
Nakalipithecus	
Sahelanthropus	*Dendropithecus*
Orrorin	*Simiolus*
Homo	*Limnopithecus*
Ardipithecus[b]	*Kalepithecus*
Praeanthropus	
Australopithecus	
Paraustralopithecus	
Paranthropus	
Pongo	
Pan	
Gorilla	

[a] Includes *Pierolapithecus* and *Anoiapithecus*
[b] Includes two genera

Late Miocene pliopithecoids are more marked than between Early Miocene Hominidea and pliopithecoids, making defining features less than clear-cut. Cranially Hominidea have a completely ossified tubular ectotympanic, which distinguishes them from both propliopithecoids and pliopithecoids but not from cercopithecoids. *Saadanius* shares a completely ossified tubular ectotympanic with crown catarrhines (Hominidea and Cercopithecidea). This has led some

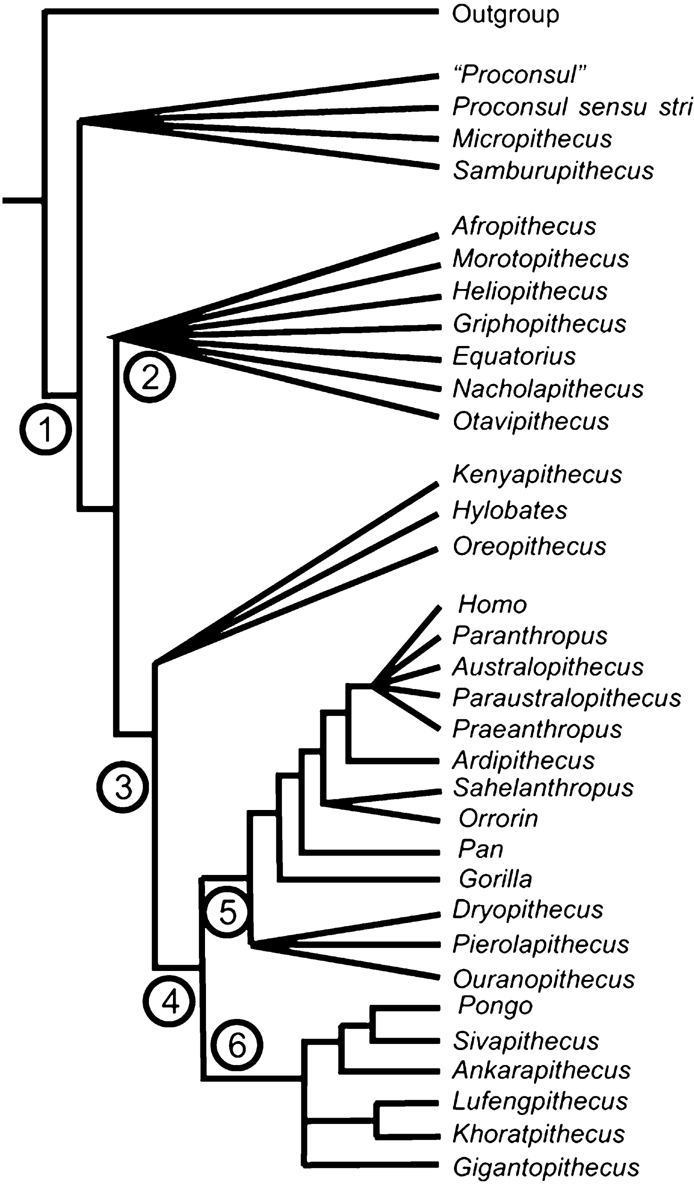

Fig. 2 Cladogram depicting the relations among most Miocene Hominidea discussed in this chapter. The cladogram is resolved only at the level of the family in many cases, except within the Hominidae, where most clades are resolved. *Numbered nodes* refer to characters or suites of characters that serve to define clades. They are not intended as comprehensive lists of synapomorphies. For clarity, *Hispanopithecus* and *Rudapithecus*, together a sister clade to *Dryopithecus*, are not shown. *Node 1*: reduced cingula, delayed life history (M1 emergence), incipient separation of the trochlea and capitulum, increased hip and wrist mobility, powerful grasping, coccyx (no tail). *Node 2*: thick enamel, increased premaxillary robusticity, further reduction in cingula,

researchers to conclude that *Saadanius* represents the common ancestor of crown catarrhines and that its age (28–29 Ma) must be the oldest possible age of divergence of the Old World Monkeys and apes (Zalmout et al. 2010). This conclusion, however, does not follow from the evidence. While *Saadanius* may preserve characters that approximate or even duplicate those of the last common ancestor of Old World Monkeys and apes, its geological age is irrelevant to the question of the age of divergence of these two lineages Pozzi et al. 2011. We have no idea how long *Saadanius* or its relatives lived before the 28–29 Ma specimens that were discovered. The taxon could be millions of years older, and in fact, we have this very problem with the pliopithecoids. Most if not all pliopithecoids are known from Eurasia, and they range in age between about 18 and 9 Ma, but they lack synapomorphies of the crown catarrhini. Using the same logic applied to the interpretation of *Saadanius*, the age of the pliopithecoids would indicate a divergence date of not more than 18 Ma for Old World Monkeys and apes, or even 9 Ma, if the last appearance of the Pliopithecoidea is taken as the divergence date. Clearly this lineage is millions of years older than the age of the oldest fossils we have of the group, and these oldest specimens remain to be discovered. Pliopithecoids represent what we call a ghost lineage, with a huge gap between their origin and first appearance in the fossil record. The same can be said of gibbons or for that matter, African apes. While we have convincing evidence of the *Pongo* clade at 12 Ma or so and the human lineage at 7 Ma or so, there is no evidence of *Pan* or *Gorilla* at all, with the possible exception of teeth attributed to *Pan* from a 500 Ka site in Kenya (McBrearty et al. 2005), many millions of years after their divergence from humans. The same is very probably true of *Saadanius*. When coupled with the convincing genetic data suggesting a divergence date of at least 30 Ma (Disotell et al. 2011), the claims of a more recent divergence based on *Saadanius* do not hold up.

Unfortunately, few Miocene Hominidea fossils preserve the portion of the temporal bone that includes the ectotympanic, so in many cases, we simply do not know if this key crown catarrhine synapomorphy was present or not. In addition, hylobatids, cranially the most primitive extant hominoid, share many features found in short-faced Old and New World monkeys, again making it difficult to tease out synapomorphies. Hominoids show a tendency to expand the length and superoinferior thickness or robusticity of the premaxilla, with increasing overlap with the palatine process of the maxilla over time, but once again this is not present in hylobatids or in early well-preserved specimens of *Proconsul*, for example (Begun 1994a). Only one specimen of Early Miocene Hominidea is

Fig. 2 (continued) increase in P_4 talonid height, possible increases in forelimb-dominated positional behaviors. *Node 3*: further “hominoidization” of the elbow. The position of *Kenyapithecus* is extremely unclear. Without this taxon, *node 3* features the numerous characters of the hominoid trunk and limbs related to suspensory positional behavior. *Node 4*: Hominidae (see text). *Node 5*: Homininae (see text). Lack of resolution of the hominini reflects continuing debate on relations among Pliocene taxa that is beyond the scope of this chapter. *Pierolapithecus* may be a stem hominid or stem hominine, as depicted here. *Node 6*: Ponginae (see text). *Gigantopithecus* is probably a pongine but the relations to other pongines are unclear complete enough to say much about the brain, and there are no unambiguous synapomorphies linking it to hominoids. The brain of *Proconsul* is similar relative to body size to both hylobatids and papionins, the Old World monkeys with the largest brains, and the sulcal pattern, while debatable, lacks most if not all hominoid features (Falk 1983; Begun and Kordos 2004). Like hylobatids, most cercopithecoids, and most mammals other than hominids, a portion of the brain of *Proconsul* occupied a large the subarcuate fossa of the temporal bone. Cranial and dental evidence also suggests that *Proconsul* was moderately delayed in terms of life history, another similarity with extant hominoids (Kelley 1997, 2004).

Postcranially, *Proconsul* more clearly represents the ancestral hominoid morphotype, though this too is the subject of debate. *Proconsul* fossils exhibit hominoid attributes of the elbow, wrist, vertebral column, hip joint, and foot, though in all cases these are subtle and disputed (Beard et al. 1986; Rose 1983, 1988, 1992, 1994, 1997; Ward et al. 1991; Ward 1993, 1997a; Begun et al. 1994; but see Harrison 2002, 1987). *Proconsul* has a suite of characters consistent with the hypothetical ancestral morphotype of the hominoids, and it should not be surprising that these are poorly developed at first, only to become more defined as hominoids evolve. In comparison with the hominoid outgroup (cercopithecoids), we can expect the earliest hominoids to show subtle indications of increased orthogrady, positional behaviors with increased limb flexibility and enhanced grasping capabilities and no tail, generalized (primitive) dentition, encephalization at the high end of extant cercopithecoids of comparable body mass, and life history variables closer to extant hominoids than to extant cercopithecoids (see chapter "▶ Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1). *Proconsul* has all of these attributes.

If these are the features that define the Hominidea, which taxa among Miocene fossil catarrhines are not Hominidea? Even the earliest cercopithecoids (victoriapithecids) are easily distinguished from hominoids (Benefit and McCrossin 2002). Pliopithecoids, often grouped with the "apes," are even more distantly related. They are clearly stem catarrhines lacking synapomorphies of all crown catarrhines including *Proconsul* and *Victoriapithecus* (Begun 2002). The most informative among these synapomorphies are the tubular ectotympanic and the entepicondylar groove (often referred to as the absence of an entepicondylar foramen). In the following sections, I will summarize current knowledge of the Miocene Hominidea, focusing on well-known taxa that serve to illustrate important events in hominoid evolutionary history (Fig. 2).

Origins of Hominidea

It is likely that hominoids originated in Africa from an ancestor that, if known, would be grouped among the Pliopithecoidea. Pliopithecoids, currently known only from Eurasia, share with all catarrhines the same dental formula and possibly with crown catarrhines a reduction of the midface, subtle features of the molar dentition, and a partial ossification of the ectotympanic tube (Begun 2002). The presence of pliopithecoids in Africa is suggestive but remains to be demonstrated

(Andrews 1978; Begun 2002; Rossie and MacLatchy 2006). The oldest and most primitive catarrhine that can lay claim to hominoid status however is African (Table 1). *Kamoyapithecus*, from the Oligocene of Kenya, differs from other Oligocene catarrhines (propliopithecoids) in being larger and having canines and premolars that more closely resemble Miocene hominoids than Oligo-Miocene non-hominoids (Leakey et al. 1995). Only craniodental material of *Kamoyapithecus* has been described, and it is so primitive as to make attribution to the Hominoidea difficult. Though it would fail to fall among the Hominoidea in a quantitative cladistic analysis due to its fragmentary preservation and primitive morphology, it makes in my view a good Hominidean precursor. Stevens et al. (2013) report on a new taxon, *Rukwapithecus*, from 25.2 Ma sediments in Tanzania. The specimen consists of a nicely preserved right mandible of a juvenile individual with the p4 to m2 erupted and the m3 still in its crypt. Unfortunately, and this is frustratingly common, no teeth can be directly compared between *Kamoyapithecus* and *Rukwapithecus*, as the latter is known only from lower postcanine teeth, none of which are known for *Kamoyapithecus*. We cannot rule out the possibility that *Rukwapithecus* is a junior subjective synonym of *Kamoyapithecus* and only more fossils will help to resolve this question. On the other hand, Stevens et al. (2013) characterize *Rukwapithecus* as the oldest known fossil ape and tentatively classify it among the nyanzapithecines, a poorly defined and possibly paraphyletic taxon that includes *Rangwapithecus* and *Nyanzapithecus*. These taxa do have some unusual features of the lower dentition, but given the tiny sample size, it is premature in my opinion to consider the "nyanzapithecines" and *Rukwapithecus* in particular to be more closely related to Middle Miocene and later hominoids than *Proconsul*, as Stevens et al. (2013) suggest. Koufos (see chapter "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3) covers some of the same fossils as covered here, with some differences in interpretation. Senut (chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3) proposes some radically different interpretations of some of the material presented here, in addition to interpretations of the latest Miocene and the Pliocene hominin fossil record that differ from any other published interpretation of which I am aware. Both authors and Schwartz (chapter "▶ Defining Hominidae," Vol. 3) employ the term hominid to mean humans and taxa more closely related to humans than to any other taxon. The vast majority of researchers employ the term as it is used here, referring to great apes and humans and all fossil taxa more closely related to these crown taxa than to hylobatids.

Proconsuloidea

Proconsul

The superfamily Proconsuloidea, as defined by Harrison (2002), includes many mainly Early Miocene taxa. As noted, in this chapter, a number of taxa from this group are interpreted to represent primitive Hominidea or hominoids. A hypothetical ancestral morphotype for the Hominidea is given in Fig. 2 (node 1). Node 1

Plate 1 *Proconsul* from the Tinderet localities of Songhor and Koru. The two *P. africanus* specimens to the *left* are male as is the *P. major* mandible to the *right*. From *left* to *right*, M 14084 (*P. africanus* type), KNM-SO 1112, M 16648. Not to scale. *P. major* is much larger

represents the bifurcation of *Proconsul* from hominoids with more apparent synapomorphies to living hominoids. *Proconsul* as described here is based mainly on the sample from Rusinga Island and Mfangano, two localities that are close together on Lake Victoria, western Kenya. These sites are often referred to as the Kisingiri *Proconsul* localities, as opposed to the Tinderet localities of Songhor, Koru, Legetet, and Chamtwara, among others. The Kisingiri include the species *Proconsul heseloni* (Walker et al. 1993) and *Proconsul nyanzae* (Le Gros Clark and Leakey 1950). The type specimen of *Proconsul africanus* (Hopwood 1933) is from Koru, and the type of *Proconsul major* (Le Gros Clark and Leakey 1950) is from Songhor, both of which are Tinderet localities (Drake et al. 1988). Historically the Tinderet localities have been considered to be older than the Kisingiri sites (Drake et al. 1988), but this new evidence indicates that there is some overlap in ages (Table 1) (McNulty personal communication). There is strong evidence that the Kisingiri species of *Proconsul* that are the basis of the description here actually belong to a different genus from the Tinderet types (see below). However, as this is not the appropriate venue to name a new genus, I will follow convention and refer to the Rusinga sample as *Proconsul*. In the end, both taxa traditionally attributed to *Proconsul* are most likely to be sister taxa, so whether it is one genus or two is only of interest to those who are working directly on this material, though when worked out it will give us a much better idea of the actual specimen composition of each taxon, which is the necessary precursor to any analysis of the paleobiology of fossil taxa (Plates 1, 2, and 3).

Postcranial Morphology

Proconsul and other proconsuloids are defined by a large number of characters. *Proconsul* is a generalized arboreal quadruped but is neither monkey-like nor apelike (Rose 1983). The following summary is mainly from Rose (1997), Ward (1997a), and Walker (1997). In addition to the characters noted that emphasized its hominoid affinities, *Proconsul* has limbs of nearly equal length (though the forelimbs were probably slightly longer than the hindlimbs), with scapula positioned laterally on the thorax and the ovoid and narrow glenoid positioned inferiorly, as in

Plate 2 “*Proconsul*” *heseloni* from Rusinga. KNM-RU 2036 on the *left* is the type specimen and is female, while the specimen to the *right* (KNM-RU 2087) is a male

Plate 3 “*Proconsul*” *nyanzae* from Rusinga. M16647 on the *right* is the type specimen and male. KNM-RU 7290 is a female

generalized quadrupeds. The thorax is transversely narrow and deep superoinferiorly, and the vertebral column is long and flexible, especially in the lumbar region. The innominate is long with a narrow ilium and an elongated ischium. The sacrum is narrow, and its distal end indicates that it articulated with a coccygeal and not a caudal vertebra, in other words *Proconsul* had a coccyx and not a tail (Ward et al. 1991).

In the details of limb morphology, *Proconsul* also combines aspects of monkey and ape morphology. *Proconsul* forelimbs lack the characteristic elongation of ape forelimbs, though this trend in ape evolution may be represented by some slight forelimb elongation in *Proconsul*. The humeral head is oriented posteriorly relative to the transverse plane, and the humeral shaft is convex anteriorly, both of which are consistent with the position of the glenoid fossa and the shape of the thorax. The distal end of the humerus lacks the enlargement of the capitulum and trochlea and other details of the hominoid elbow, but it does have a narrow zona conoidea and a mild trochlear notch. These are characters that are more strongly developed in extant apes that are universally regarded as indications of suspensory positional behavior. It is interesting that *Proconsul* shows incipient signs of apelike morphology in the elbow while lacking other more definitive indicators of orthograde or suspension. It is possible that these early, subtle changes in the elbow and in other areas of the postcranium of *Proconsul* are related to the positional demands of an animal moving around in the trees without a tail (see below).

The medial epicondyle is more posteriorly oriented as in monkeys. The proximal ends of the radius and ulna are consistent with the morphology of the distal humerus. The radial head is small and ovoid, the ulnar trochlea is narrow and has a poorly developed keel, and the radial notch is positioned anteriorly. The ulna also has a large olecranon process. All of these features are consistent with generalized pronograde (above branch) quadrupedalism as opposed to antipronograde (suspensory or below branch) (Ward 2007).

Distally, the radial carpal surface is flat and articulates mainly with the scaphoid. The ulnar head is comparatively large with a long and prominent styloid process that articulates directly with the pisiform and triquetrum, unlike living hominoids, which have greatly reduced ulnar styloids and no contact with the carpals. However, the nature of the contact between the ulnar styloid and the pisiform and triquetrum differs from that of monkeys and does suggest a greater degree of mobility, or at least a different pattern of mobility, than seen in Old World Monkeys (Beard et al. 1986). The carpals are small transversely. The scaphoid is separate from the os centrale and the midcarpal joint is narrow. The hamate hamulus is small, and the surface for the triquetrum is flat and mainly medially oriented (Beard et al. 1986). However, the manner in which the bones of the wrist come together in *Proconsul* shares attributes with monkeys and apes, making it unique. Nevertheless, in my view, the *Proconsul* wrist does provide evidence of an incipient transformation for a more stable pronograde-dominated posture to more diverse habitual postures. The metacarpal surfaces of the distal carpals are small and comparatively simple as are the corresponding surfaces on the metacarpal bases. The metacarpals are short and straight and their heads transversely narrow. The proximal ends of the proximal phalanges are slightly dorsally positioned as in palmigrade quadrupeds. All the phalanges are short and straight compared with apes, though secondary shaft features, in particular of the proximal phalanges, suggest powerful grasping (Begun et al. 1994).

The hindlimbs of *Proconsul* are also dominated by monkey-like characters. The long bones are long and slender. The femoral head is small compared to apes, but its articulation with the acetabulum indicates more mobility compared to most monkeys. The feet of *Proconsul* are monkey-like in their length-to-breadth ratio (they are narrow compared to great ape feet). *Proconsul* tarsals are elongated relative to breadth and the metatarsals long compared to the phalanges. Like those of the hands, the foot phalanges of *Proconsul* are straighter and less curved than in apes but with more strongly developed features related to grasping than in most monkeys. The hallucial phalanges are relatively robust, suggestive of a powerfully grasping big toe. Body mass estimates for the species of *Proconsul*, based mainly on postcranial evidence, range from about 10 to 50 kg (Ruff et al. 1989; Rafferty et al. 1995). The lower estimate is based in part of juvenile specimens, and it is probable that the smallest adult *Proconsul* weighed about 15 kg. In addition to morphological evidence, the range of body mass estimates in *Proconsul* from Rusinga and Mfangano strongly suggest that at least two species are represented.

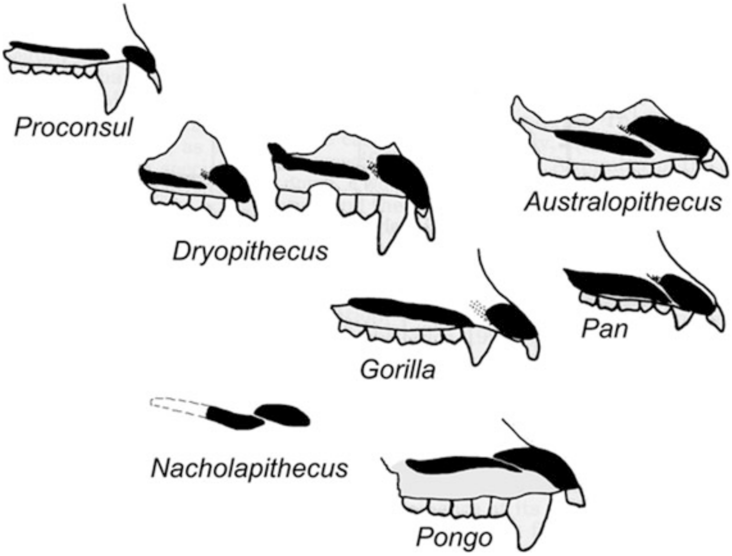

Fig. 3 Midsagittal cross section of a number of Hominidea *palates* showing some of the features described in the text. *Proconsul* has a small premaxilla and a fenestrated palate (large foramen and no overlap between the maxilla and premaxilla). *Nacholapithecus* has a longer premaxilla with some overlap. It is similar to *Afropithecus* and conceivably could be the primitive morphotype for the Hominidae. *Pongo* and *Sivapithecus* have a similar configuration but with further elongation and extensive overlap between the maxilla and premaxilla, producing a smooth subnasal floor. Hominines have robust premaxillae that are generally shorter and less overlapping than in *Sivapithecus* and *Pongo*. *Dryopithecus* is most similar to *Gorilla*, which may represent the primitive condition for hominines. *Pan* and *Australopithecus* have further elongation and overlap, but the configuration differs from *Pongo*. This morphology is suggested to be an important synapomorphy of the *Pan*/*Homo* clade (Begun 1992b) (Modified from Begun 1994)

Craniodental Morphology

As noted, *Proconsul* has a moderate amount of encephalization (comparable to hylobatids and papionins), a short face with a fenestrated palate (Fig. 3), a smoothly rounded and somewhat airorhynchous face (Fig. 4), and a generalized dentition. Morphologically, the dentition is consistent with a soft fruit diet, and microwear analysis suggests the same (Kay and Ungar 1997; chapter "▶ Dental Adaptations of African Apes," Vol. 2). The somewhat enlarged brain of *Proconsul* implies a degree of life history delay approaching the hominoid pattern (Kelley 1997, 2004; Kelley and Smith 2003; Smith et al. 2003).

One aspect of the cranium of *Proconsul* that has received some attention is the frontal sinus. Walker (1997) interprets the presence of a frontal sinus in *Proconsul* to indicate its hominid status, citing the presence of large frontal sinuses in some great apes. Other researchers have suggested that the frontal sinus is a primitive character, as it is found in *Aegyptopithecus* and many New World monkeys (Andrews 1992; Rossie et al. 2002). The confusion stems from the use of one term to describe several different characters. As Cave and Haines (1940) noted long

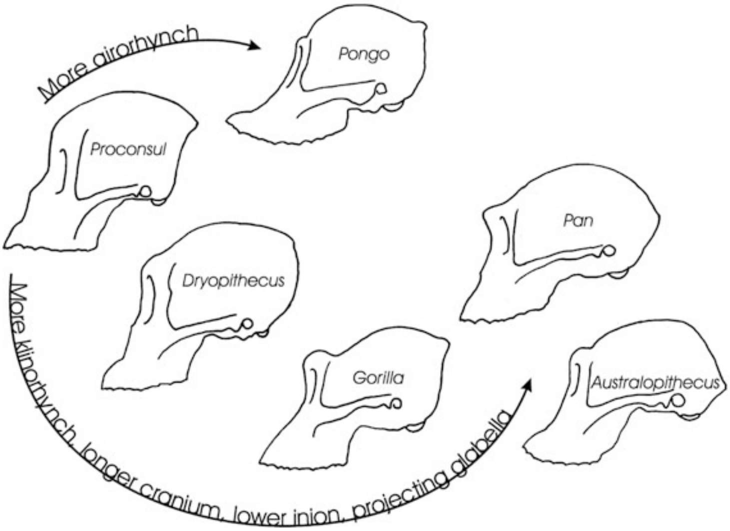

Fig. 4 Lateral views of some Hominidea *crania* showing possible changes through time. A mildly airorynch *Proconsul* may be a good ancestral morphotype for hominoid craniofacial hafting, as a similar degree of airorhynchy is also found in hylobatids (Shea 1988). *Rudapithecus* shares with other hominines neurocranial elongation (though this also occurs in hylobatids), the development of supraorbital tori, klinorhynchy, and, probably in association with the latter, a true frontoethmoidal sinus (Modified from Kordos and Begun (2001))

ago, frontal sinuses in primates have various ontogenetic origins, and it is likely that they are not homologous across the primates. New World monkeys have frontal sinuses that are outgrowths from the sphenoid sinus, as is also the case for hylobatids. On the other hand, *Pongo*, which occasionally has a frontal sinus, derives it from the maxillary sinus (see chapter "▶ Defining Hominidae," Vol. 3). African apes and humans normally have large frontal sinuses derived from the ethmoidal sinuses. "Frontal sinuses" then are actually three different characters, frontosphenoidal sinuses, frontomaxillary sinuses, and frontoethmoidal sinuses.

While it is possible to establish the ontogenetic origin of a pneumatized frontal bone in living primates, it is more difficult in fossil primates. However, the placement and size of the frontal sinuses correlate very well with their ontogenetic origin, offering a protocol for identifying the specific type of frontal sinus present in a fossil (Begun 1994a). Frontosphenoidal sinuses invade large portions of the frontal squama but not the supraorbital or interorbital regions. Frontomaxillary sinuses are infrequent in *Pongo*, but when they occur, they are associated with narrow canals or invaginations connecting the maxillary sinuses to a small pneumatization of the frontal via the interorbital space. In African apes and humans, the frontoethmoidal sinuses arise from a spreading of the ethmoidal air cells in the vicinity of nasion, resulting in large pneumatizations from below nasion into the supraorbital portion of the frontal. The actual amount of frontal pneumatization is variable, while the presence of a large sinus around nasion is constant. Therefore, while we cannot observe the development of frontal pneumatization in fossil primates, and we do not have adequate ontogenetic series to directly reconstruct this growth, we can infer the type of frontal pneumatization from its position, extent, and connection to the source sinus. In *Proconsul*, as in hylobatids, New World monkeys, and *Aegyptopithecus*, the frontal pneumatization is extensive and occupies the frontal squama, consistent with a frontosphenoidal sinus. Thus, the "frontal sinus" in *Proconsul* is a primitive character, as suggested by Andrews (1992), but for different reasons. The frontal pneumatization of *Rudapithecus*, on the other hand, conforms to the pattern seen exclusively in African apes and humans (see below).

In summary, *Proconsul* was an above branch mid- to large-sized catarrhine with a diet dominated by soft fruits and a somewhat slower life history than cercopithecoids. Encephalization may imply other similarities to hominoid behavioral or social ecology, or it may simply be a consequence of relatively large body mass and/or a slower life history (Kelley 2004; Russon and Begun 2004). The slightly enhanced range of motion in *Proconsul* limbs may imply some degree of orthogrady, it may be a consequence of the absence of a tail, of large body mass in an arboreal milieu, or, most likely, some combination of all three (Beard et al. 1986; Begun et al. 1994; Kelley 1997).

Other Possible Proconsuloids

A number of taxa are regarded by many researchers as having a probable close relationship to *Proconsul*. The three with the best evidence for affinities to the proconsuloids are *Proconsul sensu stricto*, *Micropithecus*, and *Samburupithecus*. As noted, the type species of the genus *Proconsul* is *P. africanus*. *P. africanus* and *P. major*, both from Tinderet sites, are never found together with *Proconsul* from Rusinga and are also more primitive and lack synapomorphies shared by *Proconsul* from Rusinga and other hominoids (see below). Other taxa listed in Table 2 are either more likely to be hominoids given similarities to known hominoids (*Rangwapithecus*, *Nyanzapithecus*, *Mabokopithecus*) or they are so primitive or poorly known as to make unclear their magnafamily status.

Proconsul sensu stricto

The species of *Proconsul sensu stricto* from Songhor and Koru (*P. africanus* and *P. major*) probably represent a different genus from *P. heseloni* and *P. nyanzae*, the samples on which the descriptions of *Proconsul* presented here are based. A new genus would replace *P. heseloni* and *P. nyanzae*, as *P. africanus* has priority. *Proconsul sensu stricto* from Songhor and Koru has elongated postcanine teeth, more strongly developed cingula, upper premolars with strong cusp heteromorphy, and conical, individualized molar cusps, all of which suggest that the older species are in fact more primitive. The two Tinderet species differ from each other mainly in size. Postcrania attributed to *Proconsul* from the Tinderet *Proconsul sensu stricto* localities are distinct from postcrania from the younger *Proconsul* localities such as

Rusinga, in details that have been correlated to paleoecological differences (Andrews et al. 1997). While sufficiently similar to the better-known younger *Proconsul* sample to warrant placing both in the same superfamily, the more modern morphology of the younger *Proconsul* sample will almost certainly require taxonomic recognition.

Ugandapithecus, based on the sample of *P. major*, adds to the confusion (Senut et al. 2000). *Ugandapithecus* is not a useful nomen in that it mixes a number of specimens from different localities, different sizes, and even different morphologies, and it has not been effectively compared with and distinguished from either *Proconsul sensu stricto* or the Kisingiri sample. Therefore, the nomen is not recognized here except as a junior subjective synonym of *Proconsul*. Nevertheless, it turns out that *Proconsul* as traditionally defined probably does represent more than one genus. Senut et al. (2000; see chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3) have suggested that large-bodied hominoids from Moroto, in Uganda, that is, *P. major*, may also be attributed to *Ugandapithecus* (hence the name, though the type is from Kenya), calling into question the interpretation that hominoid cranial and postcranial fossils from Moroto belong to one taxon (*Morotopithecus*). However, the evidence for more than one large hominoid genus at Moroto is not strong (see below).

Micropithecus

Micropithecus (Fleagle and Simons 1978) is a small catarrhine with comparatively broad incisors and long postcanine teeth with low cusps and rounded occlusal crests. The cingula are less strongly developed than most other Early Miocene catarrhines. Males and females exhibit marked size dimorphism. Comparisons with living catarrhines suggest a body mass of about 3–5 kg (Harrison 2002). While Harrison (2002, 2010) considers this taxon to be even more distantly related to the Hominoidea than are the Proconsuloidea, the subtly more modern features of the dentition suggest that it may belong to the Proconsuloidea. Fleagle and Simons (1978) in fact attribute *Micropithecus* to the Hominoidea, although as noted the features shared with hominoids are very subtle. If *Micropithecus* is a proconsuloid, as preferred here, it would indicate that the proconsluoids were quite diverse in body mass, as is the case in all catarrhine superfamilies.

Samburupithecus

Samburupithecus is another possible proconsuloid, known only from a large maxillary fragment from the Late Miocene of the Samburu region of Kenya (Ishida and Pickford 1997). Ishida and Pickford (1997) have suggested that *Samburupithecus* is an early member of the African ape and human clade, while others place it within the hominoids, but without specific affinities to any living clade (e.g., Harrison 2010; see chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). However, *Samburupithecus* retains many primitive characters of the Proconsuloidea. These include a low root of the zygomatic processes, a strongly inclined nasal aperture edge, the retention of molar cingula, and thick enamel with high dentine relief (Begun 2001). *Samburupithecus* is most likely to be a late surviving proconsuloid. Its unusual dental characters (e.g., large molars with individualized cusps separated by deep

Plate 4 Comparison between *Samburupithecus*, KNM-SH 8531 (*left*) and "*Proconsul*" (KNM-RU 1677a). Note the strongly developed molar cingula and the small M1 relative to M2 in both specimens. The molars are similar in overall morphology as well

narrow fissures) are reminiscent of morphological "extremes" found in terminal lineages with long evolutionary histories. *Oreopithecus*, *Gigantopithecus*, *Paranthropus*, *Daubentonia*, and *Ekgmowechashala* all share with *Samburupithecus* exaggerated occlusal features compared with other members of their respective clades. The size and occlusal morphology of *Samburupithecus* that superficially resembles *Gorilla* (Ishida and Pickford 1997) may be related in part to the fact that both are ends of long phylogenetic branches. In a pattern analogous to long branch attraction in molecular systematics, there is a tendency for separate long isolated lineages to converge in certain aspects of their morphology (Begun 2001). For whatever the reason, in its details *Samburupithecus* is primitive and more likely to belong to the proconsuloids than the hominoids (Plate 4).

Nyanzapithecines

In contrast to the phylogeny presented in Stevens et al. (2013), I consider *Rangwapithecus* and *Nyanzapithecus* to be proconsuloids and not more closely related to more modern apes. Harrison (2010) includes the nyanzapithecines among the proconsuloids, and that is the view adopted here. Nyanzapithecines as defined by Harrison (2002, 2010) include a diverse assemblage of fossil taxa ranging in dental size from somewhat smaller that *Proconsul* to the size of *Proconsul heseloni* or *P. africanus*. Several of these specimens are beautifully preserved, including the holotypes of *Rangwapithecus* and *Turkanapithecus*. There is a nicely preserved mandible of *Nyanzapithecus* as well. Yet, these taxa have proven extremely resistant to classification. I am not convinced that the Nyanzapithecinae as constituted by Harrison (2010) is a natural group. While there are superficial similarities in the occlusal morphology of the molars of all three genera and *Mabokopithecus* as well, these taxa are mostly distinguished from *Proconsul* by the complexity of their occlusal surfaces rather than being linked by morphological details. In many cases, these types of molars with more complicated patterns of crests and taller cusps that tend to be more isolated from one another occur in conjunction with selection for a more folivorous diet. This may explain in part some of what I consider to be superficial convergences in the morphology of the teeth of these taxa. In sum, I find the case for a specific relationship between *Mabokopithecus* and *Nyanzapithecus* fairly convincing, but I would not include *Rangwapithecus* or *Turkanapithecus* in the same subfamily. All of these taxa are most likely to be proconsuloids with more folivorous adaptations than other proconsuloids. As noted earlier, at this point it is premature to link the 25 Ma *Rukwapithecus* with the much younger sample of *Rangwapithecus*.

Early Hominoids

Afropithecus

A number of late Early Miocene and Middle Miocene taxa share characters with extant Hominoids and are included here in the Hominoidea. *Afropithecus* (Leakey and Leakey 1986) is known from several localities in northern Kenya dated to 17–17.5 Ma (Leakey and Walker 1997). *Afropithecus* shares an increase in premaxillary robusticity and length with most extant hominoids (Fig. 3). Like many Late Miocene and Pliocene hominids, *Afropithecus* has very thick occlusal enamel as well (Smith et al. 2003). On the other hand, similarities have been noted between *Afropithecus* cranial morphology, particularly the morphology of the midface, and that of *Aegyptopithecus*. Leakey and Walker (1997) have suggested that the unusual primitive-looking face of *Afropithecus* may be related to a specialized scerocarp seed predator adaptation. This is functionally consistent with the robust, prognathic premaxilla; large, relatively horizontal incisors; large but relatively low-crowned canines; expanded premolars; thick enamel; and powerful chewing muscles of *Afropithecus*. A similar set of features is found in modern primate seed predators such as pithecines. It may be that some of the primitive appearance of the *Afropithecus* face is homoplastic with *Aegyptopithecus*. However, another possibility is that the unusual morphology of the face of the single specimen of *Afropithecus* on which this morphological characterization is based is the result of postmortem deformation. My observations of the original specimen and other more fragmentary specimens of *Afropithecus* lead me to conclude that the type is deformed and probably resembled *Proconsul* more closely than *Aegyptopithecus*. Nevertheless, the characters noted above related to the development of the premaxilla, the implantation of the incisors, and the implantation and morphology of the canines are real differences from *Proconsul*. Thus, as with *Proconsul*, *Afropithecus* has a mosaic of primitive and derived characters (Leakey et al. 1991; Leakey and Walker 1997; Plate 5).

The large, albeit deformed, type specimen of *Afropithecus* reveals some information on neurocranial morphology. KNM-WK 16999 preserves a portion of the braincase immediately behind the orbits. Postorbital constriction is very marked, though I believe this is the result in part of postmortem deformation. However, there

Plate 5 The type specimen of *Afropithecus*, KNM-WK 16999 (*left*) and a well preserved mandible, KNM-WK 17012 (*right*). Note the lack of bone surfae around the nasal aperture and incisors and the exceptionally large interorbital area, indicative of deformation

is no doubt that the anterior temporal lines are very strongly developed. These converge to form a pronounced and very anteriorly situated sagittal crest. The small portion of the anterior cranial fossa preserved indicates a cerebrum that was constricted rostrally, lacking the frontal lobe expansion typical of extant and fossil great apes. The increased robusticity of the masticatory apparatus of *Afropithecus* in comparison with *Proconsul* is undeniable, despite some caveats related to preservational issues. The large mandibles, robust zygomatics, thickly enameled teeth, and powerfully developed attachment sites for chewing muscles all indicate that the dietary adaptations of *Afropithecus* differed significantly from those of *Proconsul*, and more closely approach those of some later Miocene apes. These differences from *Proconsul* are confirmed by more recently described specimens (Rossie and MacLatchy 2013).

Afropithecus is similar in size to *Proconsul nyanzae*, based on cranial, dental, and postcranial dimensions (Leakey and Walker 1997). *Afropithecus* postcrania are very similar to those of *Proconsul*, so much so that Rose (1993) found them essentially indistinguishable. However, *Afropithecus* postcrania are much less well known than *Proconsul*, and it is conceivable that as more fossils of *Afropithecus* are discovered, some differences from *Proconsul* will emerge. Nevertheless, given our current state of knowledge, the postcranial adaptation of *Afropithecus*, in terms of body mass and positional behavior, is *Proconsul*-like, while the craniodental anatomy is markedly distinct.

Another early hominoid taxon, *Heliopithecus*, is contemporaneous with *Afropithecus* and morphologically very similar, though it is only known from a fragmentary hemimaxilla and a few isolated teeth (Andrews and Martin 1987). Both *Heliopithecus* and *Afropithecus* share characters that are found next in the fossil record in Eurasia, which suggests that *Heliopithecus* and *Afropithecus* taxa may have a closer relationship to late Early Miocene and Middle Miocene hominoids from Europe than do proconsuloids. Certainly the most important piece of the puzzle of ape evolution to be provided by *Heliopithecus* is its geography. *Heliopithecus* is from the site of Ad Dabtiyah, in Saudi Arabia. While that sounds extraordinary, it is useful to recall that geologically the Saudi Arabian peninsula is part of the African plate, and until fairly recently much of the fauna of Africa was present in the Arabian peninsula as well. During the Early Miocene, the Arabian peninsula was much more humid than today and supported large and diverse forest communities. Given my interpretation that *Afropithecus*-like adaptations may have permitted hominoids to disperse into Eurasia in the late Early Miocene (see below), the presence of a very similar taxon on the road to Eurasia from East Africa is certainly telling.

Morotopithecus

Morotopithecus is a fossil hominoid from Uganda dated to about 21 Ma by some and 17 Ma by others (Gebo et al. 1997; Pickford et al. 2003). It is best known from a large cranial specimen including most of the palate (Pilbeam 1969). For many years, this specimen was attributed to *Proconsul major*, but it is clear that it and other specimens from Moroto are sufficiently different to justify a genus distinct from *Proconsul*. *Morotopithecus* is similar in size to *Proconsul major* and larger than *Proconsul nyanzae* and *Afropithecus*. It lacks the distinctive subnasal morphology of *Afropithecus* and has a *Proconsul*-like premaxilla that is short, gracile, and does not overlap the palatine process of the maxilla, resulting in a large incisive fenestration (Fig. 3). *Morotopithecus* has a broad palate; large anterior teeth, especially the canines, which are tusklike; a piriform aperture broadest about midway up; and an interorbital space that appears to be relatively narrow, though it is damaged. However, the most important distinction of *Morotopithecus* is the morphology of the postcrania, which are said to be modern hominoid-like. Newly described specimens of *Morotopithecus* include the shoulder joint, hip joint, and details of the vertebral column (MacLatchy 2004). Walker and Rose (1968) described the vertebrae as hominoid-like, which has been confirmed by more recent discoveries and analyses. The glenoid fossa of *Morotopithecus* suggests a more mobile shoulder joint as does the morphology of the hip joint. However, it is the hominoid-like position of the transverse processes of the vertebrae that represents the strongest evidence for the hominid affinities of *Morotopithecus*. The roots of the transverse processes of the lumbar vertebrae of *Morotopithecus* are positioned posteriorly, as in extant great apes, suggesting a stiff lower back and an axial skeleton like that of extant hominoids. However, this interpretation has not gone unchallenged, and for the time being, I consider the degree to which *Morotopithecus* was orthograde to be unresolved (Nakatsukasa 2008).

Eurasian Hominoid Origins

As noted, *Heliopithecus* and *Afropithecus* have more robust jaws and teeth than Early Miocene proconsuloids, and this may represent a key adaptation that permitted the expansion of hominoids into Eurasia at about 17 Ma, when during a marine low stand, a diversity of terrestrial mammals moved between Africa and Eurasia

(Made 1999; Begun 2001, 2009; Begun et al. 2003a, b, 2012; Nargolwalla 2009). Toward the end of the Early Miocene, the movement of the southern landmasses northward, combined with a number of other developments (the Alpine and Himalayan orogenies, the earliest appearance of the polar ice caps, and the Asian monsoons), leads to a sequence of connections and barriers to terrestrial faunal exchange (Rögl 1999a, b; Adams et al. 1999; MacLeod 1999; Hoorn et al. 2000; Zhisheng et al. 2001; Guo et al. 2002; Liu and Yin 2002; Wilson et al. 2002; Nargolwalla 2009). This period of global turbulence affected sea levels between continents cyclically such that for the remainder of the Miocene, there would be periodic connections (low stands) and disconnections (high stands) between the continents. At about 17 Ma, a low stand that had permitted the exchange of terrestrial faunas between Eurasia and Africa (the Proboscidean datum) was coming to an end but not before hominoids possibly resembling *Afropithecus* and *Heliopithecus* had dispersed from Africa into Eurasia (Heizmann and Begun 2001; Begun 2002, 2004; Begun et al. 2003a, b, 2012).

At the end of the Early Miocene, about 16.5 Ma, hominoids of more modern dental aspect first appear in Eurasia. The oldest Eurasian hominoid is cf. *Griphopithecus*, known from a molar fragment from Germany (Heizmann and Begun 2001). *Griphopithecus* (Abel 1902) is known mainly from large samples from Turkey of roughly the same age, while the type material is known from a probably later (14–15 Ma) locality, Děvínská Nová Ves, in Slovakia (Heizmann 1992; Andrews et al. 1996; Heizmann and Begun 2001; Begun et al. 2003a, b). cf. *Griphopithecus* from Engelswies in Germany is a tooth fragment that has the more modern features of being thickly enameled with low dentine penetrance (tall dentine horns did not project into the thick enamel cap as in *Proconsul* and probably *Afropithecus*). cf. is the designation for a taxon that is similar enough to another taxon for there to be a strong likelihood that they are the same, but with some formally acknowledged uncertainty. *Griphopithecus* is better known from over 1,000 specimens, mostly isolated teeth, from two localities in Turkey (Çandır and Paşalar). One species, *Griphopithecus alpani* (Tekkaya 1974), is known from both localities, while a second somewhat more derived taxon is also found at Paşalar (Alpagut et al. 1990; Martin and Andrews 1993; Kelley and Alpagut 1999; Ward et al. 1999; Kelley et al. 2000; Kelley 2002; Güleç and Begun 2003).[1]

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[1] Some researchers have suggested that the specimen from Engelsweis, which we all agree is at least 16.5 Ma, if not more than 17 Ma, is more likely to be an *Afropithecus* or a relative thereof, with no relationship to *Griphopithecus* (Casanovas-Vilar et al. 2011). These researchers are in agreement with Böhme et al. (2011) that *Griphopithecus* in Anatolia is later in time (ca. 13.5 Ma). My analysis of the biostratigraphy of the Çandır locality indicates that it is likely to be at least 16 Ma (Begun et al. 2003a). Until more research is concluded, there will remain uncertainty about the ages of the Çandır and Paşalar localities, though at 13.5 Myr this makes them much younger than previously thought. However, even if the Anatolian *Griphopithecus* sites are 3 Myr younger than Engelsweis, that is no justification for the claim that the latter must have been the result of a separate dispersal event as opposed to the simpler scenario in which hominoids with thickly enameled teeth enter Europe at 17 Ma and evolve in situ. As noted earlier, the tooth from Engelsweis more closely resembles those from Anatolia and Slovakia than it resembles *Afropithecus*.

Plate 6 *Top row*, *Nacholapithecus* palate. *Left*, lateral view, *right*, palatal view. *Bottom row*, *Nacholapithecus* mandible (*left*), *Equatorius* mandible (*right*). The *Nacholapithecus* specimens belong to the partial skeleton KNM-BG 35250, and the *Equatorius* mandible to the partial skeleton KNM-TH 28860

Griphopithecus alpani has a robust mandible with strongly reinforced symphysis; broad, flat molars with thick enamel; and reduced cingulum development compared with *Proconsul*. It retains primitive tooth proportions (small M1 relative to M2), anterior tooth morphology, and postcanine occlusal outline shape. A few fragments of the maxilla from Paşalar indicate a primitive morphology for the anterior palate (Martin and Andrews 1993). The morphology of *Griphopithecus* molars as well as their microwear indicates a diet allowing the exploitation of hard or tough fruits, though it is not clear if this means simply that they could exploit these resources when needed (a keystone resource) or if they were a favored source of food. Two postcranial specimens, a humeral shaft and most of an ulna, from the younger site of Klein-Hadersdorf, Austria, are also similar to *Proconsul* and indicate that *Griphopithecus* was a large-bodied above-branch arboreal quadruped similar in size and positional behavior to *Proconsul nyanzae* (Begun 1992a). Phalanges from Paşalar are also said to be most similar to those of *Proconsul* and extant arboreal quadrupeds (Ersoy et al. 2008) (Plates 6 and 7).

East African Middle Miocene Thick-Enameled Hominoids

Shortly after the appearance of *Griphopithecus* in western Eurasia (but see footnote 1), dispersals between Eurasia and Africa were interrupted by the Langhian transgression (Rögl 1999a). Following the Langhian, at about 15 Ma, dispersals resumed in a number of mammal lineages, probably also including hominoids (Begun et al. 2003a, b; Begun 2009; Nargolwalla 2009; Begun et al. 2012). Hominoids closely similar to *Griphopithecus* in dental morphology appear in Kenya at this time. *Equatorius* is known from 15 Ma localities in the Tugen Hills and at Maboko, both in Kenya. This taxon, previously attributed to *Kenyapithecus*, is very similar to *Griphopithecus* but has a distinctive incisor morphology and reduced cingula,

Plate 7 *Kenyapithecus* and *Griphopithecus*. *Top row*, *Kenyapithecus wickeri* (type specimen, KNM-FT 46), lateral (*left*) and occlusal (*center*) views. *Equatorius* (type specimen, M16649) occlusal (*right*). *Bottom row*, *Griphopithecus alpani* type mandible (MTA 2253) (*left*) and three upper central incisors, from *left* to *right*, "*Proconsul*" (KNM-RU 1681), *Equatorius* (KNM-MB 104) and *Kenyapithecus wickeri* (KNM-FT 49)

probably warranting a distinct genus status (Ward et al. 1999; Kelley et al. 2000; Ward and Duren 2002; *contra* Begun 2000, 2002; Benefit and McCrossin 2000). *Equatorius* is also known from a good sample of postcrania, including most of the bones of the forelimb, vertebral column, hindlimb long bones, and a few pedal elements (McCrossin 1997; Ward and Duren 2002). Like *Griphopithecus*, which is much less well known postcranially, *Equatorius* is similar to *Proconsul nyanzae* in postcranial size and morphology.

Nacholapithecus (Ishida et al. 1999) is known from deposits of the same age as *Equatorius* in the Samburu Basin of Kenya (Nakatsukasa et al. 1998). Like *Equatorius*, *Nacholapithecus* is known from a relatively complete skeleton, more complete in fact than the best specimen of *Equatorius*. From this exceptional skeleton, we know that *Nacholapithecus* is similar to other Middle Miocene hominoids in most aspects of the jaws and teeth but unique in aspects of limb morphology. While they are not especially elongated, the forelimbs of *Nacholapithecus* are more robust, that is, they are more strongly built, than are the hindlimbs. In a fascinating comparison, Ishida et al. (2004) show that *Nacholapithecus* has forelimb joints the size of a chimpanzee but hindlimb joints closer in size to those of a baboon, of much smaller body mass. The forelimbs were not elongated as in modern apes, but they were enlarged. This is difficult to understand, but it probably has something to do with some increase in the degree to which *Nacholapithecus* was loading its forelimbs relative to its hindlimbs, even if it was not suspensory. Once again, we have a weird, unique fossil ape without a modern counterpart. Kunimatsu et al. (2004) provide evidence that the anterior portion of the palate of *Nacholapithecus* is more hominid-like in its length and degree of overlap with the palatine process of the maxilla (Fig. 3). This morphology is the principal evidence for the hominoid status of this species. However, in its details, the anterior palate of *Nacholapithecus* is unlike that of hominids (see below). In my opinion, there is also evidence of some postmortem compression that may contribute to the impression that the anterior portion of the palate of *Nacholapithecus* is more modern looking than it actually was.

Otherwise, the postcranial skeleton of *Nacholapithecus* is similar to other Middle Miocene hominoids in having the general signature of a generalized, palmigrade, arboreal quadruped, but differs from *Equatorius*, also known from fore and hindlimb, in the enlarged size and robusticity of its forelimb. While not like extant nonhuman hominoids in forelimb length relative to the hindlimb, *Nacholapithecus* forelimbs are large and powerful, indicating a form of positional behavior emphasizing powerful forelimb grasping (Ishida et al. 2004). Interestingly, several wrist bones are well preserved in both *Nacholapithecus* and *Equatorius*, and they are quite similar to each other and to *Proconsul* and *Afropithecus* (personal observations).

Kenyapithecus (Leakey 1962) is the most derived of the Middle Miocene African hominoids, and may be the earliest hominid (Table 2), although I should add that it is the least well known. *Kenyapithecus* is known only from a small sample from Fort Ternan in Kenya, though a second species may be present in Turkey (see below). Like other Middle Miocene hominoids, *Kenyapithecus* has large flat molars with broad cusps and thick enamel. The maxilla of *Kenyapithecus*, however, is derived in having a high root of the zygomatic, a probable hominid synapomorphy. While McCrossin and Benefit (1997) believe that *Equatorius* and *Kenyapithecus* represent a single species, most researchers have concluded that two genera are present and that *Kenyapithecus* is derived relative to *Equatorius* (Harrison 1992; Ward et al. 1999), and that is the view adopted here. As noted, it has been suggested that *Kenyapithecus* is also present at Paşalar. If so, and if *Kenyapithecus* is indeed an early hominid, this would date the origin of the hominid family to at least 16 Ma (but see footnote 1). However, there is a roughly 3 Ma gap between possible *Kenyapithecus* at Paşalar and the type material from Fort Ternan.

One last Middle Miocene hominoid deserves mention here. *Otavipithecus* is the only Miocene hominoid known from southern Africa, from the 13 Ma site of Berg Aukas in Namibia (Conroy et al. 1992). Several specimens have been described, including the type mandible, a frontal fragment, and a few postcrania (Conroy et al. 1992; Pickford et al. 1997; Senut and Gommery 1997). It has been suggested that *Otavipithecus* has affinities to hominids (Conroy et al. 1992; Ward and Duren 2002), but it preserves primitive proconsuloid characters such as a small M_1 compared to M_2, a long M_3, parallel tooth rows, a small space for the mandibular incisors, low P_4 talonid, and tall, centralized molar cusps (Begun 1994b). Singleton (2000) carried out the most comprehensive analysis of *Otavipithecus* and concluded that it may be related to *Afropithecus*, which is broadly consistent with the placement of the taxon in Fig. 2. Like *Heliopithecus*, the most informative piece of information from the sample of *Otavipithecus* comes from its biogeography. *Otavipithecus* is a huge geographic outlier, suggesting that hominoids were widespread in equatorial and southern Africa but have yet to be found. *Otavipithecus* is morphologically somewhat atypical of Early and Middle Miocene hominoids, and I expect that when other taxa are found between Kenya and Namibia or elsewhere in Africa, they will be equally surprising.

Summary of Middle Miocene Hominoid Evolution

The radiation of Middle Miocene hominoids in Africa was relatively short-lived and less diverse than the Early Miocene radiation (see Table 1). Having apparently dispersed from Eurasia by about 15 Ma, they are mostly extinct by 12.5–13 Ma. Aside from a few fragmentary specimens that most likely represent the end of the *Proconsul* lineage (Hill and Ward 1988), hominoids would not appear again in Africa until the Late Miocene. Given the rarity of hominoid localities in the early Middle Miocene, the biogeographic hypothesis of the dispersal of Middle Miocene hominoids presented here is debatable. It is certainly possible, for example, that Early Miocene *Griphopithecus*-like fossils will be found in Africa that will show that *Equatorius*, *Nacholapithecus*, and *Kenyapithecus* all evolved in situ in Africa and that apparently earlier fossils from Eurasia are either misdated or are early offshoots of this clade with no direct relationship to later hominids (Ward and Duren 2002). In the end, perhaps the best way to think about Middle Miocene hominoids is in terms of a group of closely related genera that occupied the circum-Mediterranean region and the contiguous regions north into Germany and south into Kenya (with one known long distance dispersal into Namibia). Movements within the geographic area of these taxa were probably very complex and numerous over time, but from this melting pot of Middle Miocene thickly enameled hominoids, the first true hominids appear.

Early Hominids

While *Kenyapithecus* shares a synapomorphy with the Hominidae (position of the zygomatic root), the first clear-cut hominids are known from Eurasia and share numerous cranial, dental, and postcranial synapomorphies with living hominids. This is the most important body of data supporting the Eurasian origins hypothesis. If that hypothesis is incorrect, we need to account for the absence of fossil hominids in Africa (which could just be bad luck) and also the presence of apparent hominid synapomorphies in both the Asian and European hominid fossil records.

The extant Hominidae is divided into two subfamilies, Ponginae and Homininae, and the earliest representatives of both subfamilies are roughly contemporaneous. The earliest hominines are represented by *Dryopithecus* and possibly *Pierolapithecus* and *Anoiapithecus* (see below). Much better known and with clearer hominine synapomorphies are *Rudapithecus*, *Hispanopithecus*, and *Ouranopithecus* (see chapter "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3). The earliest pongines are represented by *Ankarapithecus*, *Sivapithecus*, and relatives. Miocene hominines are known from western Eurasia, while Miocene pongines are known from South and East Asia, reflecting the basic biogeographic division of the two hominid subfamilies today [but see Kelley and Gao (2012)].

Fossil Pongines

The oldest sample of fossils widely interpreted as pongine is of *Sivapithecus* from the middle Chinji formation in the Siwaliks of Pakistan (Raza et al. 1983; Rose 1984, 1989; Kappelman et al. 1991; Barry et al. 2002). Specimens referred *Sivapithecus indicus* that are known to come from the middle Chinji formation share characters with later *Sivapithecus* and other hominids including reduced or absent molar cingula; relatively large M1; reduced premolar cusp heteromorphy; long, buccolingually compressed canines; broad-based nasal aperture; elongated and robust premaxilla partly overlapping the maxilla; and, as in *Kenyapithecus*, a high position to the zygomatic root. They share specifically with later *Sivapithecus* fewer clear-cut characters, such as probably strongly heteromorphic upper incisors (known only from the roots), and broad, flat cusped molars with thick enamel, though these characters are also found in most other Middle and many Late Miocene hominoids. One specimen of Chinji *Sivapithecus*, GSP 16075, represents a portion of the palate with the connection between the maxilla and premaxilla partially preserved. The maxillary-premaxillary relationship is highly diagnostic of *Sivapithecus* and the pongine clade, and the morphology of the Chinji specimen has been interpreted to share characters of this complex (Raza et al. 1983; Ward 1997b; Kelley 2002). However, while the specimen does have a relatively elongated, horizontal, and robust premaxilla, the area of the incisive fossa and foramen is not preserved. In the absence of this region, it is difficult to distinguish Chinji *Sivapithecus* from later *Sivapithecus*, including later *Sivapithecus indicus*, to which it is assigned, versus another pongine, *Ankarapithecus*. *Ankarapithecus* preserves a morphology of the anterior palate that lacks the synapomorphies of *Sivapithecus* and *Pongo* (Begun and Güleç 1998), and this may also be the case for the Chinji jaw. Resolution of this uncertainty would help to clarify the biogeography of pongine origins (see below).

Sivapithecus

Sivapithecus Craniodental Evidence

Most of the *Sivapithecus* samples, including the best-known specimens with the clearest evidence of pongine affinities, are from younger localities of the Siwaliks of India and Pakistan, dated between 10.5 and 7.5 Ma (Barry et al. 2002). In the following section, I discuss *Sivapithecus* in some detail because it is in many ways critical to understanding Late Miocene hominoid evolution. Three species are generally recognized in this sample, the best known of which is *Sivapithecus sivalensis* (Lydekker 1879), from localities ranging in age from 9.5 to 8.5 Ma (Kelley 2002). In addition to the characters outlined above, S*ivapithecus sivalensis*

Plate 8 GSP 15000, the best preserved specimen of *Sivapithecus*. To the *right* is a lateral view of the *face* without the mandible (Courtesy of Milford Wolpoff)

is known from a suite of cranial characters strongly indicative of pongine affinities (Pilbeam 1982). These include unfused tympanic and articular portions of the temporal bone; a posterosuperiorly directed zygomatic arch with deep temporal and zygomatic processes; vertically oriented frontal squama; supraorbital costae or rims; a narrow interorbital space; elongated nasal bones; tall, narrow orbits; wide, anteriorly oriented zygoma; narrow, pear-shaped nasal aperture; externally rotated canines; long, horizontally oriented nasoalveolar clivus that is curved along its length but flat transversely; and a subnasal region with the posterior pole of the premaxilla merging into the anterior edge of the maxillary palating process to form a flat, nearly continuous subnasal floor (Fig. 3) and a strongly concave facial profile from glabella to the base of the nasal aperture. *Sivapithecus* is also likely to have been airorhynchous (having a dorsally deflected face), as in *Pongo* (Fig. 4). All of these and other characters are described in more detail in Ward and Pilbeam (1983), Ward and Kimbel (1983), Ward and Brown (1986), Brown and Ward (1988), and Ward (1997b). *Sivapithecus sivalensis* is not identical to *Pongo* in cranial morphology, however, even if the similarities are striking and detailed. *Sivapithecus sivalensis* is more robust than similarly sized (female) *Pongo* in features related to the masticatory apparatus, including aspects of the zygomatic and temporal bones, maxillary robusticity, and molar morphology. The molars in particular are easily distinguished from those of *Pongo* in having thicker enamel and in lacking the complex pattern of crenulations seen in unworn *Pongo* molars. However, overall the number of derived characters shared with *Pongo* is impressive (Ward 1997; Kelley 2002) (Plates 8, 9, and 10).

Sivapithecus indicus (Pilgrim 1910) is the oldest species, and if the middle Chinji fossils are included, it would range from 12.5 to 10.5 Ma (Kelley 2002). It is the smallest species, at least in terms of dental size, and appears to have a slightly shorter nasoalveolar clivus or premaxilla compared with *Sivapithecus sivalensis* (see above). *Sivapithecus parvada* (Kelley 1988) is considerably larger than the other species and is known from the Nagri formation locality Y311, about 10 Ma. *Sivapithecus parvada* males are about the dental size of female gorillas. The upper central incisors are especially long mesiodistally, the M_3 is larger than the M_2, the premolars are relatively large, and the symphysis of the mandible is very deep (Kelley 2002).

Plate 9 *Sivapithecus* palates. GSP 15000 to the *left* and YPM 13799 (formerly *Ramapithecus*) to the *right* (Courtesy of Milford Wolpoff)

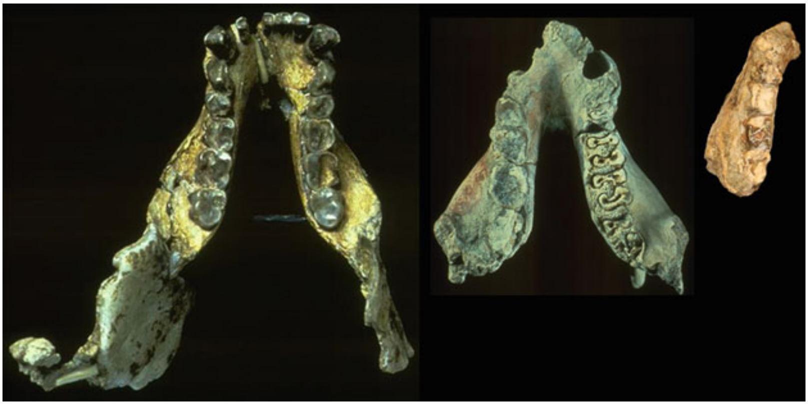


Plate 10 *Sivapithecus* mandibles, showing substantial diversity in size and morphology. The two specimens to the *left* courtesy of Milford Wolpoff. From *left* to *right*, GSP 15000, GSP 9564, M. 15423

Sivapithecus Postcrania

Sivapithecus postcrania have been described in many publications (Pilbeam et al. 1980, 1990; Rose 1984, 1986, 1989; Spoor et al. 1991; Richmond and Whalen 2001; Madar et al. 2002). They combine a mixture of characters, some suggesting more palmigrade postures and others suggestive of more suspensory positional behavior (see chapter "▶ Postcranial and Locomotor Adaptations of Hominoids," Vol. 2).

This has been interpreted by some to indicate that *Sivapithecus* is more primitive than any living hominoids, all of which, even humans, share numerous characters of the shoulder and forelimbs related to suspensory behavior or an ancestry of suspensory behavior (Pilbeam 1996, 1997; Pilbeam and Young 2001, 2004). This view, also shared by McCrossin and Benefit (1997), has dramatic implications for the interpretation of the hominoid fossil record. All Late Miocene hominoids, including *Sivapithecus*, share many characters of the cranium and dentition with living hominoids. If *Sivapithecus* is more primitive than extant hominoids, given its apparently primitive postcrania, then all the apparently derived hominid features of *Sivapithecus* would have evolved in parallel in *Sivapithecus*, and as these authors suggest, by extension in all Late Miocene hominoids (*Oreopithecus*, *Dryopithecus*, *Rudapithecus*, *Ouranopithecus*, *Lufengpithecus*, etc.). These parallelisms include not only craniodental morphology but also details of life history and, as it turns out, many postcranial characters as well. In fact, the apparently primitive characters of *Sivapithecus* postcrania are small in number compared with the large number of clearly derived hominid characters from throughout the skeleton and known biology of all Late Miocene hominids. Rather than rejecting the hominid status of *Sivapithecus* and other Late Miocene hominids because not all of their postcranial morphology is strictly hominid or even extant hominoid-like, it is much more likely that these few characters reflect mosaic evolution of the hominid skeleton, uniquely derived features of the anatomy of *Sivapithecus*, as well as some parallelism in extant hominoids (Begun 1993; Begun et al. 1997; Begun and Kivell 2011; see below).

Sivapithecus postcrania, though they have been the subject of more discussion related to phylogeny, are actually less well known than those of *Proconsul*, *Equatorius*, or *Nacholapithecus*. The following is summarized mainly from Rose (1997), Richmond and Whalen (2001), and Madar et al. (2002). Much more information is available from all the references cited earlier. Two species of *Sivapithecus* are known from the humerus, which is unlike that of modern hominoids in the curvature of the shaft and the development of the deltopectoral plane. The bicipital groove is also broad and flat and suggests a posteriorly oriented humeral head, as in the Early and Middle Miocene Hominidea described earlier. However, the humerus has such an unusual morphology that the orientation of the head, which is already somewhat difficult to predict from bicipital groove position (Larson 1996), cannot be reconstructed with great confidence. Nevertheless, the morphology of the proximal humerus in *Sivapithecus* is suggestive of some form of pronograde quadrupedalism as seen, for example, in extant cercopithecoids. If the humeral head were oriented more posteriorly, it would also be consistent with a scapula that is placed on the side of a compressed rib cage, as in typical mammalian quadrupeds, and unlike extant hominoids (Rose 1989; Ward 1997a). No direct evidence is available for the thorax or any part of the axial skeleton of *Sivapithecus*, however, so this will also have to await further discoveries. The deltopectoral plane and the curvature of the shaft of the humeri in *Sivapithecus* are quite strongly developed compared with most cercopithecoids and indicate in my view a unique form of positional behavior that is neither extant hominoid nor extant cercopithecoid-like (Madar, et al. 2002). The distal end of the humerus is in the main hominoid-like, including a well-developed trochlea separated from the capitulum by a deep, well-defined groove (the zona conoidea), though in a few details of the posterior surface, there are similarities to *Proconsul* and *Kenyapithecus* (Rose 1997). Overall, however, the functional morphology of the elbow of *Sivapithecus* is most like the hominoid elbow in its ability to resist movements other than flexion and extension at the elbow joint, a hallmark of the Hominoidea (Rose 1988).

The *Sivapithecus* forearm is poorly known, especially the proximal portions of the ulna and radius, which would help to more fully understand the *Sivapithecus* elbow. A juvenile radial shaft is known that is described as *Proconsul*-like, though as a juvenile, it is not clear to what extent we might expect any hominoid-like characters, such as curvature and the nature of the ligamentous/muscular insertions, would be expressed. On the other hand, the few carpal bones that are known show a mixture of hominoid and non-hominoid features. The capitate of *Sivapithecus* has a somewhat expanded and rounded head, as in great apes, but overall is transversely narrow and elongated proximodistally compared with great apes. The joint surface for the third metacarpal is irregular as in great apes. The hamate is similar in length/breadth proportions and has a less strongly projecting hammulus than do great ape hamates (Spoor et al. 1991). The joint on the hamate for the triquetrum is oriented as in gorillas and also most other non-hominoid anthropoids, and its shape suggests a stabilizing function at the wrist, which differs fundamentally from the typical mobility of the ulnar side of the wrist in extant hominoids. The proximal end of a first metacarpal is similar in morphology to hominids and Early Miocene Hominidea in being saddle-shaped, a configuration considered to represent a good compromise between mobility and stability in a wide variety of positions. The manual phalanges are long and curved, with strongly developed ridges for the flexor muscles and their sheaths. One complete phalanx has a relatively deep and somewhat dorsally positioned articular surface for the metacarpal head, which is more typical of palmigrade quadrupeds. However, it is not completely clear if this is from a hand or a foot, and if the latter is the case, a similar morphology exists in some hominoids as well.

Begun and Kivell (2011) undertook a reanalysis of the carpal bone of *Sivapithecus* in light of recent discoveries of carpal bones of *Rudapithecus* (see below). They concluded that there are a number of terrestrial and even knuckle-walking characteristics of the capitate and hamate of *Sivapithecus*, though the capitate and hamate of *Sivapithecus* are nevertheless easily distinguished from those of African apes. The authors suggest that if the *Sivapithecus* species to which these carpals belong (*S. sivalensis* for the capitate and *S. parvada* for the hamate) did knuckle-walk, they did so in a manner that was biomechanically different from extant African apes (see chapters "▶ The Hunting Behavior and Carnivory of Wild Chimpanzees," Vol. 2, "▶ Great Ape Social Systems," Vol. 2 and "▶ Origin of Bipedal Locomotion," Vol. 3). It is worth remembering of course that African apes today are biomechanically distinct from one another in their knuckle-walking.

Whatever this means in terms of the big picture of hominoid evolution is unclear, but one mystery that is potentially solved by this analysis is the biogeography of the Miocene pongines (see below).

The hindlimb of *Sivapithecus* is less well known but generally more similar to extant hominoids than the forelimb. The femur is known from proximal and distal ends but not from the same individual (Rose 1986; Madar et al. 2002). The hip joint as represented by the femoral head and neck was mobile in many directions, though it has a well-developed fovea capitis, unlike *Pongo*, which is highly distinctive (but not unique) in lacking a ligamentum teres of the femur and thus its attachment site to the femur, the fovea capitis. The distal end of the femur preserves evidence of a knee joint that is consistent with this interpretation, implying a knee joint loaded in positions away from the sagittal plane. The knee also has a number of features allowing for rotation of the leg and foot to adjust the lower extremity to a variety of positions close to and further away from the center of mass (Madar et al. 2002). In all of these features, the femur is more like that of hominoids than other anthropoids.

Other hindlimb elements include several tarsal bones, phalanges, and a well-preserved hallucial skeleton (Conroy and Rose 1983; Rose 1984, 1986, 1994). The tarsals are perhaps more like those of great apes than any other part of the postcranium of *Sivapithecus* (Rose 1984; Madar et al. 2002), indicating the presence of a broad foot, able to assume many positions but stable in all of them, and supportive of body mass loading from many directions. The hallux or big toe is strikingly robust, much more so than in *Pongo*, and indicates a strongly developed grasping capability in the foot. The phalanges are also by and large hominoid-like, with well-developed features related to powerful flexion of the toes, a critical function in antipronograde activities (climbing as well as suspension).

***Sivapithecus* Phylogeny and Paleobiology**

Overall, the morphology of *Sivapithecus* strongly supports a close phylogenetic relationship to *Pongo* but an adaptation that differed from *Pongo* in important aspects. Microwear suggests that *Sivapithecus* had a diet that was similar to that of chimpanzees, while gnathic morphology suggests more of a hard-object diet (Teaford and Walker 1984; Kay and Ungar 1997; chapter "▶ Dental Adaptations of African Apes," Vol. 2). Perhaps this reflects a capacity to exploit fallback or "keystone" resources in times of scarcity. Most hominoids are known to practice this strategy (Tutin and Fernandez 1993; Tutin et al. 1997). The case of gorillas may be most relevant to the question of the diet of *Sivapithecus*. Most gorillas have diets similar to chimpanzees but are able to exploit terrestrial herbaceous vegetation (THV) in lean seasons when soft fruit is less available or in contexts in which they are sympatric with chimpanzees (Tutin and Fernandez 1993; Tutin et al. 1997). The microwear results may reflect the preferred and most common components of the diet, while the morphology of the jaws and teeth may reflect a critical adaptation to a keystone resource on which survival would depend during stressful periods (see chapters "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3 and "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1).

Postcranial evidence clearly indicates that *Sivapithecus* was not orang-like in its positional behavior. In fact, it was unique; there are probably no living analogues. *Sivapithecus* combines clear indications of pronograde forelimb postures and a palmigrade hand position with more antipronograde activities such as vertical climbing and clambering implied by elbow joint stability over a wide range of flexion/extension, powerful grasping hands and feet, an especially powerful hallux, and hindlimbs capable of wider ranges of joint excursions than in extant pronograde quadrupeds (Madar et al. 2002). It is difficult to imagine exactly what the positional behavior of *Sivapithecus* might have been like.

One constant in the postcranial functional morphology of *Sivapithecus* is arboreality. Perhaps *Sivapithecus* used its powerful limbs in climbing and bridging or clambering activities, spreading the limbs across multiple supports to access smaller branches. In a sense, it is orang-like without the suspension. While *Sivapithecus* managed to distribute its considerable body mass across the tops of several branches, orangs do the same but from below. In large animals, the advantage to suspension is added stability on horizontal supports, since they otherwise need to generate very high levels of torque to stay atop a branch (Grand 1972, 1978; Cartmill 1985). Orang males are larger than *Sivapithecus* and may be beyond the threshold where pronograde limb postures are possible in the trees. The fact that the proximal half of the humerus of *Sivapithecus*, while similar to that of a pronograde quadruped, is exceptionally robust, with extremely well-developed shoulder muscle attachments, may be an indication of a unique approach to this problem.

Sivapithecus does share numerous postcranial features, especially of the elbow and hindlimb, with extant hominoids and *Dryopithecus*. It is therefore possible that the more monkey-like morphology of the proximal humerus and portions of the hands and feet are actually homoplasies with cercopithecoids caused by the adoption of more pronograde postures in a hominoid that evolved from a more suspensory ancestor (Begun et al. 1997). This requires many fewer homoplasies than the alternative hypothesis that all extant hominoid characters in all Late Miocene hominoids are homoplasies (Pilbeam 1996, 1997; McCrossin and Benefit 1997; Pilbeam and Young 2001, 2004). There is some evidence from the functional morphology of *Sivapithecus* to support the hypothesis that its form of pronograde arboreal quadrupedalism is actually superimposed on a suspensory hominoid groundplan (see chapter "▶ Origin of Bipedal Locomotion," Vol. 3).

The problem of angular momentum causing instability in a large mammal standing on top of a branch is alleviated in part by spreading the limbs apart on a wide support, or across several supports, which *Sivapithecus* seems to have been capable of doing (Madar et al. 2002). It can also be all alleviated by placing the center of mass closer to the support, which is suggested for *Griphopithecus* (Begun 1992a), and may have also occurred in *Sivapithecus*, as a consequence of its habitually more laterally placed limbs (Madar et al. 2002). The positioning of the limbs more laterally in hominoids is part of the suite of characters related to trunk morphology and scapular position. It is not facilitated by monkey-like trunks and scapular positions, which promote more parasagittal limb movements. Finally, an important response to angular momentum is to increase the torque generated by the limbs on the support, to prevent excessive excursions from a balanced position, especially when a single support of only modest size is used, again suggested to be an aspect of the positional behavior of *Sivapithecus* (Madar et al. 2002). Higher torque results from more powerful gripping, also characteristic of *Sivapithecus* (Madar et al. 2002), and may have been boosted by especially powerfully developed shoulder joint adduction and medial rotation, particularly if the shoulder is in a relatively abducted position to begin with, as in hominoids.

The morphology of the proximal half of the humerus in *Sivapithecus* is consistent with very powerful adduction and medial rotation by deltoideus and pectoralis major. These muscles left extremely prominent scars on the humerus of *Sivapithecus*. If the arm of *Sivapithecus* were positioned as in extant hominoids, laterally on a posteriorly positioned scapula, the adduction and medial rotation capacities of deltoideus and pectoralis would be increased by increasing the relative mass of the clavicular portion of deltoideus, which is unknown in *Sivapithecus*. However, in addition to the need for powerful muscles, which existed in *Sivapithecus*, these functions would also be enhanced by other attributes known in *Sivapithecus*. The extension of the muscles along the shaft distally and the possible decreased humeral neck torsion would increase the moment arm for these muscles in adduction and reposition the insertions of these muscles medially, possibly to make more of the deltoideus available for adduction and medial rotation. The strong mediolateral curvature of the shaft may result from high mediolateral bending stresses that would result from very powerful shoulder adduction on a fixed limb. The proximal shaft is also very broad mediolaterally, suggestive of strong mediolaterally directed stresses. While speculative, it is certainly conceivable that the upper part of the forelimb of *Sivapithecus* was less monkey-like than generally perceived and may not imply that much of the trunk was of the primitive anthropoid type. A small number of autapomorphies of the shoulder of *Sivapithecus* may have allowed this taxon to practice a relatively efficient form of arboreal pronograde quadrupedalism while maintaining the capacity for many of the antipronograde activities of hominoids, though probably not for frequent upper limb below-branch suspension. This hypothesis is functionally consistent with the morphology of the *Sivapithecus* postcranium in general and is certainly more parsimonious than the hypothesis that would interpret all Late Miocene hominoid characters as homoplasies (Begun and Kivell 2011).

Ankarapithecus

Aside from some material from Nepal attributed to *Sivapithecus* (Munthe et al. 1983), *Sivapithecus* is known only from India and Pakistan. Specimens from central Anatolia, Turkey, once attributed to *Sivapithecus* (Andrews and Tekkaya 1980) are now assigned to *Ankarapithecus*, following the original conclusions of Ozansoy (1957, 1965). *Ankarapithecus meteai* is known from a male palate and mandible from two different individuals and a female partial skull (mandible and face) from a third locality, all close to each other in location and geological time (Kappelman et al. 2003). Begun and Güleç (1995, 1998) resurrected the nomen *Ankarapithecus* based mainly on the morphology of the premaxilla and the

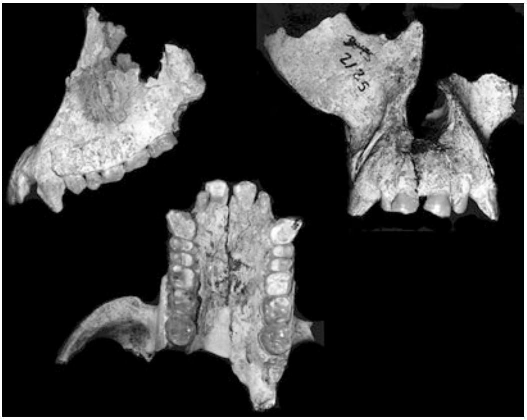


Plate 11 *Ankarapithecus* (MTA 2125)

relationship between this bone and the maxilla but concluded that *Ankarapithecus* is nonetheless in the pongine clade. Alpagut et al. (1996) and Kappelman et al. (2003) described newer and much more complete fossils of *Ankarapithecus* and concluded that it is a stem hominid (sharing a common ancestor with both pongines and hominines). The new fossils discovered and described by these authors include the region around the orbits, which lacks some of the characters of *Sivapithecus*. The interorbital region is intermediate in breadth between *Pongo*, with the narrowest interorbitals, and African apes and the orbits themselves are broad rather than tall and narrow. Alpagut et al. (1996) and Kappelman et al. (2003) also interpret the supraorbital region as a supraorbital torus, characteristic of African apes and humans and some European Late Miocene taxa, and they interpret a frontal sinus in the cranium of *Ankarapithecus* as a frontoethmoidal sinus. These authors see the mixture of hominine and pongine characters as an indication that *Ankarapithecus* precedes their divergence (Plate 11).

Craniodental Evidence

The frontal sinuses in *Ankarapithecus* appear to be confined to the frontal squama and do not invade the frontal supraorbital region from a broad expansion of the ethmoidal sinuses. They are positioned and developed as in extant taxa with frontal pneumatizations derived either from the sphenoidal or maxillary sinuses and are unlike those derived from the ethmoid (see above discussion). The frontal pneumatization in *Ankarapithecus* is unlikely to be a frontoethmoid sinus and thus is not a synapomorphy of the hominines. The supraorbital region, while robust, is morphologically similar to the robust supraorbital costae of large orangs or *Cebus* and also unlike the bar-like supraorbital tori of African apes. Thus, the supraorbital region of the *Ankarapithecus* cranium is more pongine than hominine-like and, like the maxilla, probably represents the primitive morphology for the pongines (see below).

In *Ankarapithecus*, the premaxilla, the portion of the palate with the alveoli for the incisors and the mesial half of the canines, is unlike that of *Sivapithecus* and more like that of African apes. The premaxilla is long, but it does not overlap the palatine process of the maxilla to fill the incisive fossa to the degree seen in *Sivapithecus*. Instead, the subnasal fossa is stepped (there is a drop between the base of the nasal aperture and the floor of the nasal cavity) into an incisive fossa that is most like that of some chimpanzees, a relatively large depression opening into a canal (the incisive canal that runs between the premaxilla and maxilla to exit on the palatal side via the incisive foramen). *Rudapithecus* has a similar configuration of the subnasal fossa, incisive canal, and incisive foramen, though the fossa is larger and the canal is shorter in length and larger in caliber, as in some gorillas (Begun 1994a; Fig. 3). The premaxilla of *Ankarapithecus* is curved or convex anteroposteriorly as in *Sivapithecus*, African apes, and *Rudapithecus*, but it is also convex transversely, as in African apes and *Rudapithecus* unlike *Sivapithecus*, which has a transversely flatter premaxilla. In all of these features, *Ankarapithecus* expresses a condition intermediate between pongines and hominines, which I consider primitive for the pongines (Begun and Güleç 1998). Alpagut et al. (1996) and Kappelman et al. (2003) have suggested that these characters indicate that *Ankarapithecus* precedes the divergence of pongines and hominines and is thus a stem hominid. Other features of the morphology of *Ankarapithecus* resemble pongines more clearly, including canine implantation, zygoma size and orientation, orbital margin morphology, nasal length, and dental morphology. Overall, *Ankarapithecus* most closely resembles *Sivapithecus* and *Pongo* but retains a more primitive palatal morphology that suggests it is at the base of the pongine clade.

Postcranial Evidence

Some postcrania of *Ankarapithecus* are known, including a well-preserved radius and two phalanges (Kappelman et al. 2003). A femur tentatively identified as primate is more likely in my opinion to be from a carnivore. The radius shares characters with extant great apes including features of the radial head and a comparatively long radial neck (Kappelman et al. 2003). Other hominoid-like features described or figured in Kappelman et al. (2003) but not identified as hominoid-like by these authors include a proximodistally compressed and more circular radial head, a deep radial fovea, flat as opposed to concave shaft surface along the anterior surface, a more distal origin of the interrosseous crest, and a smooth distal dorsal surface. The specimen actually strikes me as quite hominoid-like with a few features more normally associated with large non-hominoid anthropoids, a pattern more or less in keeping with other Late Miocene hominoids. The phalanges are said to be relatively straight and thus non-hominoid-like, but only distal portions are preserved. They too strike me as more hominoid-like than Kappelman et al. (2003) suggest, given its distal shaft robusticity, dorsopalmar compression, and distopalmarly projected condyles. The curvature and ridges for the flexor musculature are said to be poorly developed compared with hominoids, but this may be related to many factors (preservation, age, digit attribution).

Overall, *Ankarapithecus* is characterized by many features found in other pongines and is probably the most basal known member of that clade. Like *Sivapithecus*, it was much more massive in the development of its masticatory apparatus than *Pongo*, and its postcranium, though very poorly known, suggests arboreality and at least some features of hominoid-like antipronograde positional behaviors, but probably lacking the degree of suspension seen in dryopithecins, *Oreopithecus*, and extant hominoids (but see Kappelman et al. 2003).

Other Probable Fossil Pongines

Indopithecus-Gigantopithecus

Extremely large fossil hominoids, larger than any extant primate, have been known from Asia since the early part of the twentieth century. *Gigantopithecus blacki* (von Koenigswald 1935) is a Pleistocene taxon known from numerous isolated teeth and a few mandibles. It is recent enough to be outside the purview of this review and has been described many times elsewhere. *Sivapithecus giganteus* (Pilgrim 1915) is the oldest nomen attributed to samples from the Late Miocene of South Asia that may be related to *Gigantopithecus*. This sample, only known from a lower M3 from the Late Miocene of the Siwaliks, is mainly distinguished from *Sivapithecus* by size. When a mandible with teeth of similar size was found, a new species, *Gigantopithecus bilaspurensis*, was named, but more recently most researchers have combined the mandible with the type of *Sivapithecus giganteus* (the lower molar), thus making the new combination *Gigantopithecus giganteus* (Kelley 2002). Von Koenigswald (1949) proposed the nomen *Indopithecus* for the M3. In my view, the type of *G. bilaspurensis* is sufficiently distinct from Pleistocene *Gigantopithecus* that I place both the mandible and the M3 in *Indopithecus*, making the new combination *Indopithecus giganteus*. The jaws and teeth of *Indopithecus* are larger than any *Sivapithecus*, and the only known mandible is distinctive in having reduced anterior tooth crown heights and molarized or enlarged premolars. *G. blacki*, on the other hand, is larger still and has highly complicated postcanine occlusal morphology and relatively even larger mandibles and smaller anterior teeth. Because *I. giganteus* and *G. blacki* share characters of the lower jaws and teeth that appear commonly during the course of hominoid evolution (in fact, in many other mammal lineages as well), the relationship between the two is uncertain. Jaws and teeth in general, and mandibles in particular, are magnets for homoplasy in primate evolution (Begun 1994b, 2007), and this may be another example. In the end, the morphology of the jaw and teeth of *Indopithecus* much more closely resembles that of *Sivapithecus*, while certain dental proportions more closely resemble *Gigantopithecus*. Given the age and morphological differences, I prefer to recognize two genera, though I do recognize that they are closely related. The most parsimonious hypothesis is that *I. giganteus* is a primitive member of the *Gigantopithecus* clade and that the strong similarity to *Sivapithecus* in the molars, apart from size, suggests that it is the sister clade to that taxon (Table 1, Plate 12).

Lufengpithecus

Thousands of fossils, mostly isolated teeth, are known from a number of localities in Yunnan Province, southern China. These are attributed to the genus *Lufengpithecus* (Wu 1987). *Lufengpithecus* is most commonly recognized as a

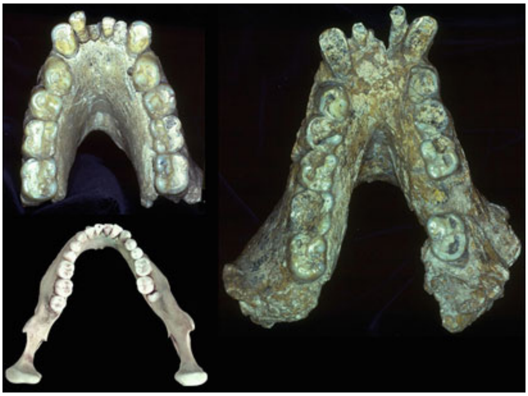


Plate 12 Two mandibles of *Gigantopithecus* compared with a modern human mandible. *Gigantopithecus* images courtesy of Milford Wolpoff

pongine. Kelley tentatively recognizes three species of *Lufengpithecus*, distinguished mainly by size and geography (each is known from a single site). *Lufengpithecus* shares a few cranial characters with other pongines including a small, pear-shaped nasal fossa, aspects of the implantation of the canine roots in the maxilla, a deep canine fossa, supraorbital costae, and anteriorly oriented zygoma (Schwartz 1997 and personal observations). However, while it lacks many of the detailed similarities of the face between *Sivapithecus* and *Pongo*, its teeth are much more like those of *Pongo* than *Sivapithecus* in details of occlusal morphology, including the unusual presence of highly complex wrinkling or crenulations (Kelley 2002). The face of *Lufengpithecus* is unlike those of *Sivapithecus* and *Pongo* in having broad orbits, a broad interorbital space, a comparatively short premaxilla, high crowned incisors and canines, and compressed and very tall crowned male lower canines. Though very damaged, my impression is that the nasal floor is unlike the smooth floor of *Sivapithecus* and *Pongo* but possibly more similar to the morphology in *Ankarapithecus*. There are intriguing similarities between *Lufengpithecus* and dryopiths, especially in the incisors and premaxilla, and Kelley and I have independently reached the conclusion that they might be more closely related to one another than *Lufengpithecus* is to pongines. This, however, is a hypothesis that needs a lot more investigation, and for now I follow Kelley (2002) in placing *Lufengpithecus* among the pongines (Plates 13 and 14).

L. lufengensis (Xu et al. 1978) from a site near Shihuiba, in Lufeng county, is the best-known species of the genus and is also known from a number of postcranial remains including fragments of a scapula, clavicle, radius, first metatarsal, and two phalanges. None have been published in detail, but all of these specimens show clear indications of modern hominid morphology associated with suspensory positional behaviors (personal observations). This is especially true of the phalanges, which are strongly curved and bear the markings of powerful flexor tendons. The metatarsal is similar to that of *Sivapithecus* in its relative robusticity.

Until the fossils attributed to *Lufengpithecus* are published in detail, it will be impossible to be confident in assessing their taxonomic and phylogenetic relations. At this point, it seems likely that *Lufengpithecus* is a pongine and probably a sister

Plate 13 Female (*upper left*, PA 586) and male (*upper right*, PA 548) mandibles of *Lufengpithecus* in occlusal view, and, *below*, an anterior view of the male. Note the high crowned and narrow anterior dentition

Plate 14 Two *Lufengpithecus* babies. To the *left*, from Yuanmou (YV 0999) and to the *right*, from Shuitangba (ZT 299) (Courtesy of Jay Kelley)

taxon to the *Pongo*-*Sivapithecus*-*Ankarapithecus* clade. However, the generally more *Pongo*-like morphology of the molar occlusal surfaces and the more clearly hominoid-like morphology of the postcrania are enigmatic and suggest caution in interpreting evolutionary relationships. Kelley and Gao (2012) describe a juvenile specimen of *Lufengpithecus* from a different locality, Yuanmou, also in Yunnan Province. The Yuanmou specimen is interpreted by these authors as having more similarities with dryopithecins than previously supposed for *Lufengpithecus*, which is consistent with my impressions of the adult specimens from Shuhuiba. However, we both come short of concluding that there is definite evidence of a phyletic link between *Lufengpithecus* and the dryopithecins. Interpreting the morphology of a taxon from a juvenile specimen can be very tricky. More detailed comparisons between the Yunnan Province *Lufengpithecus* samples and those of dryopithecins from Europe are needed to determine if there really are phylogenetic connections between the two groups of hominids independent of the Siwalik taxa. This, however, would represent a dramatic development in our understanding of Late Miocene ape biogeography and would falsify an observation I made some years ago about the separation of the Asian and European samples (Begun 2005). Another possibility of course is that the Yunnan samples represent another lineage of hominid not specifically related to any living great ape (Ji et al. 2013). Only more detailed comparisons among these samples will help to resolve this issue.

Khoratpithecus

Three samples of Southeast Asian Miocene hominoids have recently come to light. Chaimanee et al. (2003) describe a Middle Miocene sample of hominoids from Thailand they originally attributed to a species of *Lufengpithecus*. The age of the locality is not completely certain, and it is possible that the fauna could be correlated with a more recent magnetostratigraphic interval, but for now the sample is considered to date to the late Middle Miocene or early Late Miocene (13.5–10 Ma). However, on the basis of more recently discovered Late Miocene hominoid fossils from Thailand, Chaimanee et al. (2004) described a new genus, *Khoratpithecus*, and revised their previous taxonomic conclusions to include the Middle Miocene taxon in the newly named genus as well. The fossils, a sample of isolated teeth and a well-preserved mandible, are very similar to *Lufengpithecus* but show a number of differences in the anterior dentition and lower jaw (Chaimanee et al. 2004). Chaimanee et al. (2004) interpret *Khoratpithecus* to be more closely related to *Pongo* than is any other pongine, mainly based on the shared derived character of a missing anterior digastric muscle. More fossils are needed to test this hypothesis more fully. The greater significance of these discoveries is the location, in Thailand, and the possibly early age, Middle Miocene. In 2011 the same research group described a new species of *Khoratpithecus* from Myanmar (formerly Burma), to the northwest of Thailand (i.e., in the direction of the Siwaliks of India and Pakistan) (Jaeger et al. 2011). The three species of *Khoratpithecus* are represented only by a small number of mandibles and isolated teeth, and it is not clear if three different species are represented, but they do appear to be distinct from *Sivapithecus* and *Lufengpithecus*.

All four genera of Asian great apes described here range in age from possibly as old as 13.5 Ma to possibly as young as 6 Ma. If the dates are correct, *Khoratpithecus ayeyarwadyensis*, from Myanmar, is the oldest of this group and is roughly contemporary with *Kenyapithecus* from Fot Ternan, Kenya. *Lufengpithecus lufengensis* from Shuhiba (Yunnan Province, China) and *Indopithecus* from the Siwalik Hills are the youngest, at about 6–7 Ma, and are roughly contemporaneous with *Sahelanthropus*, from Chad, the earliest known hominin.

The Earliest Fossil Hominines: The Dryopithecins 1

At about the same time that hominids appear in Asia, they make their first appearance in Europe. As is the case with the earliest pongines, the earliest hominines lack a number of synapomorphies of living hominines (African apes and humans) and are less distinct from related non-hominines than are more recently evolved hominines. This has led naturally to differences of opinion regarding the systematics of this group (see chapters "▶ Defining Hominidae," Vol. 3 and "▶ Hominoid Cranial Diversity and Adaptation," Vol. 2). There are three main interpretations of the evolutionary relations among the taxa included here in the Homininae. As noted, some researchers conclude that no known Eurasian Late Miocene taxon has a specific relationship to extant hominoids (Pilbeam 1996, 1997; McCrossin and Benefit 1997; Pilbeam and Young 2001, 2004). Most researchers, however, accept the hominid status of these fossil taxa but are divided as to their interrelationships. Some researchers (Andrews 1992) have concluded that European Late Miocene hominids are best viewed as stem hominids, preceding the divergence of hominines and pongines. Others interpret most or all Eurasian hominines to be members of the pongine clade (Moyà-Solà et al. 1995). Finally, some researchers interpret most or all European hominids to be hominines, although there is disagreement among them as to the precise pattern of relations (Bonis and Koufos 1997; Begun and Kordos 1997; see chapter "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3). As my interpretation falls with the last group, this will be reflected in this chapter. I will however attempt to outline the major arguments from each perspective.

Nomenclatural History

The taxonomic history of *Dryopithecus* and the dryopithecins is very complicated (see Begun 2002 for a more complete history). At one time, most of the well-known taxa described here were attributed to *Dryopithecus* (*Proconsul*, *Sivapithecus*, *Ouranopithecus*, *Ankarapithecus*, *Griphopithecus*). More recently *Dryopithecus* was restricted to the sample European great apes from Spain, France, Germany, Austria, Hungary, and Georgia that all share features in common with African apes, in particular thinly enameled teeth with less robust jaws than *Sivapithecus* or *Ouranopithecus*. This was the consensus when the first version of this review was published in 2007. Since then the concept of *Dryopithecus* has become even more narrowly defined. As of this writing, *Dryopithecus* is restricted more or less to the original sample from St. Gaudens, a mandible from Austria and a maxilla from Spain. The important distinctions between *Dryopithecus* and most of the other samples that have until recently been attributed to *Dryopithecus* are age and morphology. All *Dryopithecus*, along with *Pierolapithecus* and *Anoiapithecus*, are more primitive in dental morphology (persistent cingula, small first molars, short premolars, robust canines) (Begun et al. 2012; Alba 2012). Postcranially, *Pierolapithecus* is more primitive than the later-occurring *Hispanopithecus* and *Rudapithecus* (see below). *Dryopithecus*, *Pierolapithecus*, and *Anoiapithecus* all occur in the Middle Miocene. Later-occurring and more modern-looking dryopithecins are all from the Late Miocene in Europe.

Specimens from the Middle Miocene of Spain have been attributed to *Dryopithecus* but also to two new taxa, *Pierolapithecus* and *Anoiapithecus*. The latter is known only from a distorted facial fragment, while the former is known from many parts of a skeleton, though unfortunately the face is seriously damaged. Because *Dryopithecus sensu stricto* is known only from male mandibles, it is extremely difficult to compare it with *Pierolapithecus* and *Anoiapithecus*, both of which are known mainly from upper teeth and postcrania. There is a mandibular fragment of *Anoiapithecus* that can be compared directly with *Dryopithecus*, and in my opinion, the differences between the two samples do not warrant a genus level distinction. *Pierolapithecus* is not known from lower teeth or jaws, and it is impossible to compare this sample with *Dryopithecus*. In addition, when they were first described, each of these taxa was assigned to different hominid clades.

Pierolapithecus and *Anoiapithecus* were first described as stem hominids, predating the divergence of pongines and hominines (Moyà-Solà et al. 2004, 2009a). *Dryopithecus*, when it was discovered at Hostalets, was first described as a hominine and possibly a sister clade to *Gorilla* (Moyà-Solà et al. 2009b). In addition, *Hispanopithecus*, also from the Vallès Penedès but from younger deposits (see below), was first described as a pongine. This represents three separate hominid clades present in a relatively restricted temporal and geographic span, which I consider unlikely. The most current interpretation of all of these taxa places them in the Ponginae (Alba 2012, Fig. 8, p. 265), though this author acknowledges that other interpretations, including the alternatives that they are all hominines or stem hominids, are possible. The practical difficulties in comparing *Pierolapithecus*, *Anoiapithecus*, and *Dryopithecus* to each other, given the few comparable parts preserved (see below), led me to be skeptical that three different genera and possibly three different clades can be effectively identified from these samples. The fact that all three Middle Miocene genera were found within a few kilometers of one another from essentially the same time period and same geological formation made me even more skeptical that three different genera are represented. All three are Middle Miocene and are more primitive than Late Miocene apes including *Hispanopithecus*. However, this is not the place for a taxonomic revision of these genera, so I will use the nomena originally proposed by the describers while noting that they are probably all closely related and possibly all *Dryopithecus*.

Dryopithecus fontani

Dryopithecus is the first-named taxon, and it is agreed by most researchers that this taxon is Middle Miocene and more primitive than Late Miocene European great apes. There is disagreement as to whether or not other early hominids taxa lived in Western Europe during the same time as *Dryopithecus*. *Dryopithecus* was first identified from St. Gaudens, on the northern slopes of the French Pyrenees (Lartet 1856). *Dryopithecus sensu stricto*, that is, *D. fontani*, is only known from three mandibles, a few isolated associated teeth, and a humeral shaft, all from St. Gaudens. Two isolated teeth from La Grive, also in France but in a geologically completely different context (Alpine as opposed to Pyrenean), are also traditionally attributed to *Dryopithecus*. These sites are considered to be Middle Miocene, based exclusively on their fauna, and the apes from these sites are more primitive dentally than apes that occur later on in Europe.

Dryopithecus fontani is known from three male mandibles and a humerus, all from the same locality in France, a female mandible from Austria, and a partial face from Spain (Begun 2002; Begun et al. 2012; Moyà-Solà et al. 2009b). Two isolated upper teeth from La Grive in France are also usually attributed to *D. fontani*. The mandibles and their dentitions are typically hominid in being comparatively robust with well-developed symphyseal tori, large incisors, compressed canines, elongated postcanine teeth with peripheralized cusps and lacking cingula, P_4 with trigonids and talonids of nearly equal height, and molars of nearly equal size, especially M1 and M2. The teeth of all *Dryopithecus* are thinly enameled with dentine horns penetrating well into the enamel caps. *D. fontani* is distinguished from other species of *Dryopithecus* in having a mandible that shallows (becomes lower compared to breath) distally, a high frequency of buccal notches on the lower molars, and comparatively robust lower canines.

The more recently described material attributed to *Dryopithecus* from Catalonia include a palate that cannot be directly compared with the fossils from France and Austria but does allow a comparison with *Anoiapithecus* and *Pierolapithecus*. Alba (2012) maintains that the morphological differences among these three samples are sufficient to justify the recognition of three different genera, all of which he places within the ponginae. In my view, the differences are minor and the samples, while including well-preserved specimens, are small, making it very difficult to assess ranges of variation within each group. This being the case, I think it is more likely that a single genus is represented, and by the rule of taxonomic priority, that taxon would be *Dryopithecus* (Begun et al. 2012).

Dryopithecus fontani is also known from a humeral shaft from the type locality that has been described as chimpanzee-like (Pilbeam and Simons 1971; Begun 1992a). It is the only nearly complete humerus of the genus. It is comparatively long and slender with poorly developed muscle insertion scars and a slight mediolateral and anteroposterior curvature. Neither the proximal nor the distal epiphyses are preserved, but the diaphysis preserved close to each epiphysis is hominoid-like. Proximally, it is rounded in cross section with a bicipital groove position suggesting some degree of humeral torsion (but see Rose 1997; Larson 1998). Distally, it is mediolaterally broad and anteroposteriorly quite flat, with a large, broad, relatively shallow olecranon fossa (Begun 1992a).

Finally, the proximal end of a femur has been tentatively attributed to *Dryopithecus* (cf. *Dryopithecus*). This specimen has been described as less suspensory than *Hispanopithecus*, with indications of a more quadrupedal form of locomotion (Moyà-Solà et al. 2009b). If this is truly *Dryopithecus*, this interpretation is somewhat at odds with the interpretation of suspensory locomotion based on the humerus, but as we see very often in the fossil record, different anatomical regions evolve somewhat independently, leading to morphological mosaics that have no analogues among living taxa.

Pierolapithecus catalaunicus

The best-known Middle Miocene hominine genus is represented by the very nicely preserved partial skeleton of *Pierolapithecus* (Moyà-Solà et al. 2004). The specimen, from northern Spain, is dated to 11.93 Ma (Casanovas-Vilar et al. 2011). The specimen includes most of a face which, though distorted, preserves nearly all the teeth and many informative facial characters. It also includes a partial postcranial skeleton, the most informative parts of which are some lumbar vertebrae, ribs, and a number of hand and foot bones. Moyà-Solà et al. (2004) interpret *Pierolapithecus* as a basal or stem hominid. More recently, Alba (2012) prefers the hypothesis that *Pierolapithecus* is a pongine. Moyà-Solà et al. (2004) cite the lumbar vertebrae, which preserve evidence of a hominoid-like vertebral column and by extension rib cage. This is indicated by the position of the lumbar transverse processes, placed more posteriorly in hominoids to stiffen the lower back (Ward 1993). However, the morphology of the lumbar vertebrae in *Pierolapithecus* is more hylobatid-like, extant hominids having even more posteriorly positioned transverse processes. Other aspects of the postcranium that clearly support the hominoid status of *Pierolapithecus* include ribs, indicative of a broad, anteroposteriorly compressed rib cage, robust clavicle, and a wrist morphology indicating no direct contact between the carpus at the triquetrum and the ulna (Moyà-Solà et al. 2004). These features are shared with all extant hominids. Hylobatids are unique in their carpal/ulnar contact, having a large intervening articular meniscus (Lewis 1989). The homologous surface of the triquetrum in *Pierolapithecus* indicates a great ape and not a hylobatid configuration.

The carpals in general are hominid-like in their overall morphology, including relative size, robusticity, and general pattern of the orientation of the joint surfaces. The lunate, triquetrum, and hamate in particular closely resemble small chimpanzees, but it is not clear if these are derived characters for hominines or hominids. Moyà-Solà et al. (2004) describe the phalanges of *Pierolapithecus* as being relatively shorter, less curved, and with metacarpal joint surfaces facing more dorsally than in *Rudapithecus* and *Hispanopithecus*, clearly suspensory hominines, which they interpret to mean that *Pierolapithecus* had a palmigrade hand posture (see also Alba et al. 2010). At the same time, the attributes of the thorax and hand suggest antipronograde (suspensory) limb positions, which is somewhat contradictory. They resolve this dilemma with the suggestion that *Pierolapithecus* was a powerful vertical climber but not suspensory. This is similar to the suggestion made earlier regarding *Sivapithecus*, though the morphology of the phalanges does not in fact rule out suspension. The phalanges are curved compared with most arboreal primates and have strongly developed flexor muscle attachments, even if these are not so strongly expressed as in *Hispanopithecus* and *Rudapithecus* (Begun and Ward 2005). Deane and Begun (2008) concluded that the phalanges of *Pierolapithecus* were in the range of curvature seen in *Hylobates*, *Pongo*, *Rudapithecus*, and *Hispanopithecus*. Based on phalangeal curvature, Deane and Begun (2010) considered *Pierolapithecus* to be more suspensory than Old World monkeys and African apes but less than in Asian apes.

Moyà-Solà et al. (2004) interpret various craniodental attributes of *Pierolapithecus* to reflect its stem hominid status as well. The face is prognathic with an enlarged premaxilla. The zygomatic root is high, the nasal aperture broad, and the postcanine teeth have a typical hominid morphology (elongated, relatively large M^1, absence of cingula, reduced premolar cusp heteromorphy, buccolingually large incisors, compressed canines). The premaxilla is expanded compared with early and exclusively Middle Miocene hominoids and appears to have an overlap posteriorly with the maxilla, as in hominids. However, according to these authors, it lacks the distinctive attributes of either the hominine of pongine clade.

Some of the distinctive attributes of *Pierolapithecus* are clearly related to distortion. The glabella is unlikely to have been as posterior as it appears, the midface is clearly badly damaged and was not as prognathic as in *Afropithecus*, despite what the authors suggest, and the premaxilla is obviously displaced relative to the palatine process of the maxilla (Begun and Ward 2005). In my view, the face much more closely resembled *Hispanopithecus*, though it is still distinct enough to justify a separate genus. The similarities with *Afropithecus* are probably related to a similar pattern of distortion (see above).

All in all, *Pierolapithecus* closely resembles *Dryopithecus*, known from contemporaneous localities in France and Austria, and *Hispanopithecus* and *Rudapithecus*, known from younger localities in Spain and Hungary. Based on this level of similarity, a consensus is emerging that all of these taxa belong in the tribe Dryopithecini (Begun et al. 2012; Alba 2012).

Attributes of the postcrania and dentition are more primitive in *Pierolapithecus* and justify a separate genus from Late Miocene *Hispanopithecus* and *Rudapithecus*. There is evidence to suggest that *Pierolapithecus* is a stem hominine and not as Moyà-Solà et al. (2004) conclude, a stem hominid, or as Alba (2012) concludes, a stem pongine (Begun and Ward 2005; Begun 2007, 2009; Begun et al. 2012). Details of dental morphology are strikingly similar to other dryopithecins (*Dryopithecus*, *Rudapithecus*, *Hispanopithecus*). Despite the unusually small M^3 and elongated upper canine, most of the teeth could easily be mistaken for those of other dryopithecins and show features distinctive for that tribe, including relatively tall crowned and mesiodistally narrow upper incisors, compressed canines, premolars with prominent cusps separated by a broad deep basin, and molars with marginalized or peripheralized, relatively sharp cusps. The contact between the premaxilla and the maxilla appears to also have been very similar to *Rudapithecus* in being stepped with only a modest degree of overlap between the two (Alba 2012; Begun 2007, 2009; Begun et al. 2012). The supraorbital region, though described by Moyà-Solà et al. (2004) as having thin supraorbital arches, actually closely resembles *Rudapithecus* and *Hispanopithecus* specimens from Spain and Hungary, with subtle tori emerging from a more prominent glabella. In my view, *Pierolapithecus* is close to the common ancestor of the Hominidae but already shares a common ancestor with the Homininae (Begun and Ward 2005; Begun 2009). Its postcranial morphology, however, is probably very close to that of the hominid ancestral morphotype (Fig. 2).

Anoiapithecus

Anoiapithecus is the third genus of Middle Miocene hominine from Hostalets de Pierola (Moyà-Solà et al. 2009a). As noted, it was originally interpreted to be a stem hominid and more recently a stem pongine. The stem hominine attribution is largely on the basis of its short face (hence the trivial name *brevirostris*). The dental

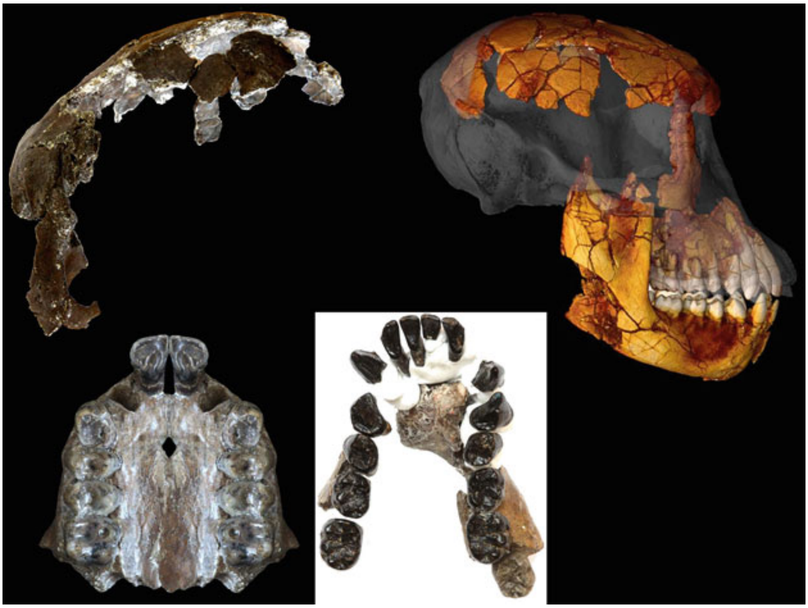


Plate 15 *Rudapithecus*. The two crania (RUD 77, *left* and RUD 200, *right*) include the most complete brain cases of a European hominine. The RUD 200 image is a virtual reconstruction superimposed on a chimpanzee skull (Courtesy of Philipp Gunz). RUD 12 (*bottom left*) is a female left hemi-palate mirror imaged to make a complete palate. RUD 14 (*bottom right*) is juvenile male mandible

morphology, which is the best preserved parts of *Anoiapithecus*, is very similar to other dryopithecins, and without the facial portions, it would certainly be assigned to *Dryopithecus*. The facial portions that are preserved are quite fragmentary, and I am doubtful that a reliable reconstruction of the palate relative to the upper part of the face can be achieved. When the most complete and well-preserved parts of the *Anoiapithecus* specimen are considered, their similarity with *Dryopithecus* is undeniable. Whether or not the reconstruction provided in Moyà-Solà et al. 2009a holds up will depend in my view on the recovery of a more completely preserved face.

Late Miocene European Hominines: The Dryopithecins 2

Hispanopithecus

Hispanopithecus crusafonti (Begun 1992c) is known from a sample of isolated teeth and a palatal fragment from Can Ponsic and a well-preserved mandible from Teuleria del Firal, both in northern Spain and both dated to between 10.4 and 10 Ma (Casanovas-Vilar et al. 2011). *H. crusafonti* is dentally similar to other dryopithecins but has distinctive upper central incisors, a more robust mandible lacking the distal shallowing of *Dryopithecus*, upper molars of nearly the same size, and a number of other subtle features of dental morphology (Begun 1992c) (Plates 15, 16, 17, and 18).

Plate 16 RUD 44 in medial view. Note the stepped subnasal fossa (blue lines) between the alveolar process and the palatine process of the maxilla (yellow lines)

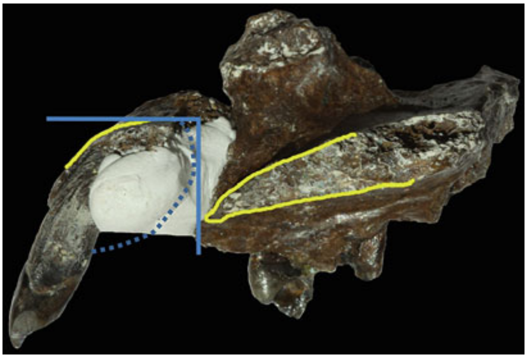
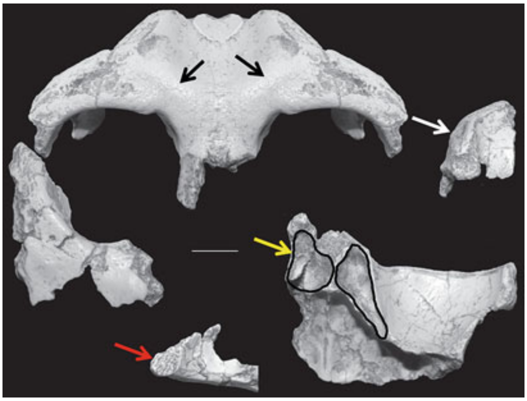


Plate 17 *Hispanopithecus* (IPS 18000). The frontal bone in anterior view is mirror imaged from the *left side*. *Black arrows*, rudimentary supraorbital tori; *white arrows*, torus in lateral view; *yellow arrow*, frontal sinus penetrating into the interorbital space; *red arrow*, zygomatic portion of the frontozygomatic suture



Hispanopithecus laietanus (Villalta and Crusafont 1944) is known from several slightly younger sites in Spain. Dentally, it is smaller but similar to other dryopithecins and lacks the unique dental characters of *H. crusafonti*. It is the best-known species of the genus. Like *H. crusafonti*, *H. laietanus* has tall, relatively narrow upper central incisors, though not to the degree seen in *H. crusafonti*. The mandible is relatively robust. A partial cranium of *H. laietanus* displays numerous hominid cranial characters (broad nasal aperture base, high zygomatic roots, shallow subarcuate fossa, and probable enlarged premaxilla with maxillary overlap, although the specimen is damaged in that area). A few hominine characters are found on this specimen as well (supraorbital tori connected to glabella, frontoethmoidal sinus, inclined frontal squama, and thin enamel) (see Alba 2012 for a different interpretation).

The most significant specimen of *H. laietanus* is a partial skeleton, an exceptional and important specimen (Moyà-Solà and Köhler 1996). The most significant features of the postcranial skeleton of *H. laietanus* are the numerous and unambiguous indications of both well-developed suspensory positional behavior and clear hominid synapomorphies. These include elongated forelimb; large hands with

Plate 18 *Hispanopithecus* reconstruction (*left*) and *Rudapithecus* in three fourth view (*right*)

powerful, curved, elongated digits; comparatively short and robust hindlimb; and a hominid-like lumbar region. Other attributes interpreted to be present in this partial skeleton, such as an elongated clavicle and limb proportions approaching those of *Pongo*, are based on fragmentary evidence and are less reliable. The specimen has some unusual features for a hominid such as short metacarpals, but overall it is quite modern. The humerus, though fragmentary, is like that of *D. fontani* and unlike that of *Sivapithecus*. While there is universal agreement that *Hispanopithecus* is orthograde and suspensory, there is disagreement on the degree to which it was suspensory (Almécija et al. 2007; Deane and Begun 2008, 2010; Alba et al. 2010).

Rudapithecus hungaricus

Rudapithecus hungaricus Kretzoi, 1969 was named based on the sample of hominines from Rudabánya, Hungary (Begun and Kordos 1993). Most researchers rejected to generic distinctiveness of *Rudapithecus*, preferring to include the Rudabánya sample in *Dryopithecus brancoi* (Begun and Kordos 1993), myself included. In the second half of the nineteenth century, shortly after the initial discovery and description of *Dryopithecus fontani*, additional fossil hominoid teeth began to turn up in Germany. These were eventually assembled to define the new species, *D. brancoi* (Schlosser 1901), though not before considerable taxonomic shuffling (see Begun 2002 for more historical details). *D. brancoi* is based on an isolated M_3 which, while not the ideal type specimen, can be effectively distinguished from the other species. To help in species identification, the species diagnosis was revised by Begun and Kordos (1993) based on the excellent sample from Rudabánya, Hungary. This was the majority view through 2009. At that time, researchers working on the Spanish and Hungarian samples had independently come to the conclusion, as described earlier, that *Dryopithecus* as originally described should include only Middle Miocene more primitive European hominines, while the Late Miocene taxa traditionally attributed to *Dryopithecus* should be reassigned to their original nomena (*Rudapithecus* and *Hispanopithecus*). The nomenclatural history of these samples is described more fully in Begun (2009).

Table 3 Great ape and African ape craniodental character states of *Rudapithecus*

Great ape character states	African ape character states
Labiolingually thick incisors	Biconvex premaxilla
Compressed canines	Stepped subnasal fossa
Elongated premolars and molars	Patent incisive canals
M1 = M2	Broad, flat nasal aperture base
No molar cingula	Shallow canine fossa
Reduced premolar cusp heteromorphy	Supraorbital torus
High root of the zygomatic	Inflated glabella
Elongated midface	Frontal sinus above and below nasion
Broad nasal aperture below the orbits	Projecting entoglenoid process
Reduced midfacial prognathism	Fused articular and tympanic temporal
Elongated, robust premaxilla	Broad temporal fossa
Premaxilla-palatine overlap	Deep glenoid fossa
Shallow subarcuate fossa	Elongated neurocranium
Enlarged semicircular canals	Moderate alveolar prognathism
Large brain	Klinorhynchy
High cranial base (Begun 2004)	

Rudapithecus hungaricus is only known from Rudabánya (Hungary) and is dated to about 10 Ma. Six other localities in Germany, Austria, and Georgia may also contain *Rudapithecus*, but as the specimens are all isolated teeth, it is difficult to be certain. *Rudapithecus* shares all the hominid characters already described for other Late Miocene hominids, but the cranium is better preserved in this taxon than in any other and provides additional details (Table 3).

Rudapithecus shares with other dryopithecins all the details of canine and postcanine tooth morphology outlined above. It shares relatively narrow and labiolingually thick upper central incisors with other dryopithecins, though not to the degree seen in *H. crusafonti*. *Rudapithecus* preserves a few details of the face and many details of the neurocranium and basicranium, with further evidence of its hominid status. The zygoma are high, prominent, and oriented anterolaterally, as in hominines, and the number and position of the zygomaticofacial foramina is variable (this character has been proposed as one that could establish the pongine affinities of *Hispanopithecus*, but the configuration in *Rudapithecus* is hominine-like (Kordos and Begun 2001)) The neurocranium is large, with a reconstructed cranial capacity in the range of extant chimpanzees (*Rudapithecus* is the only Late Miocene hominid for which cranial capacity reconstruction is possible from direct measurements of the brain case [in two individuals]) (Kordos and Begun 1998, 2001; Begun and Kordos 2004).

Among the hominine characters preserved in the cranial sample of *Rudapithecus* are a relatively low and elongated neurocranium, with the inion displaced inferiorly (Table 3). The interorbital and supraorbital regions have sinuses that are largest above glabella. Glabella is prominent and continuous with small supraorbital tori separated from the frontal squama by a mild supratoral sulcus (Begun 1994a).

The temporal bone, in addition to preserving evidence of a shallow subarcuate fossa (a hominid character), suggests fusion of the articular and tympanic portions and preserves details of the temporomandibular joint found only in hominines (Kordos and Begun 1997). RUD 200 (also known as RUD 197-200), the best preserved cranium of a dryopithecin, is the first to include a well-preserved neurocranial and facial skeleton in connection and shows clearly that the cranium of *Dryopithecus* was klinorhynch (having a ventrally deflected face), which it shares with African apes among the hominoids (Kordos and Begun 2001; Fig. 4).

The nasoalveolar clivus or premaxilla is hominine like in its orientation, size, surface anatomy, and relations (Fig. 3). It is biconvex, long compared to Early Miocene Hominidea and hylobatids (proportionally equal in length to *Gorilla*), with a posterior pole that is elevated relative to the nasal floor, giving a stepped morphology to the subnasal fossa (Begun 1994a; Fig. 3). The resulting incisive fossa of the subnasal floor is deep and well defined, the incisive canal is short and large in caliber, and the incisive foramen on the palatal side is comparatively large. This suite of characters is found in *Gorilla* as well, which suggests that this is the ancestral morphology for hominines. *Pan* and *Australopithecus* share the synapomorphic condition of a more elongated but still biconvex premaxilla, which along with their spatulate upper central incisors and neurocranial morphology is among the most important morphological synapomorphies of the chimpanzee-human clade (Begun 1992c).

Rudapithecus is well represented by postcrania, including a distal humerus that is hominid-like in all details related to trochlear and capitular morphology as well as having broad and shallow fossae for the processes of the radius and ulnae (see above). The ulna is robust with a strongly developed trochlear keel and a radial facet orientation that indicates forearm bones positioned for enhanced antipronograde postures (Begun 1992a). The scaphoid is *Pongo*-like in morphology and was not fused to the os centrale, as it is in African apes and humans (Begun et al. 2003c). The capitate is large with a complex metacarpal articular surface, as in African apes, but the head is comparatively narrow and the bone overall is elongated compared to African apes, again more like the condition in *Pongo* and *Sivapithecus*. The triquetrum and pisiform provide evidence that the ulna did not contact the medial carpals in any way, an important synapomorphy of the great apes and humans. The phalanges are long, strongly curved, and marked by sharp ridges for the flexor musculature, indicative of suspensory positional behavior (Begun 1993). The femora of are short, with a large head, long neck, and extremely robust shaft, consistent with the hominoid pattern, and again especially similar to *Pongo*. The foot is also apelike in its broad, flat talar body and mobile but large entocuneiform and hallux.

Ouranopithecus

A large hominid sharing characters of *Dryopithecus* and *Sivapithecus* was first described from northern Greece and attributed to the genus *Dryopithecus* (to which *Sivapithecus* was also attributed at the time) (Bonis et al. 1975). Soon it became clear that the sample from Greece was distinct from both *Sivapithecus* and *Dryopithecus*,

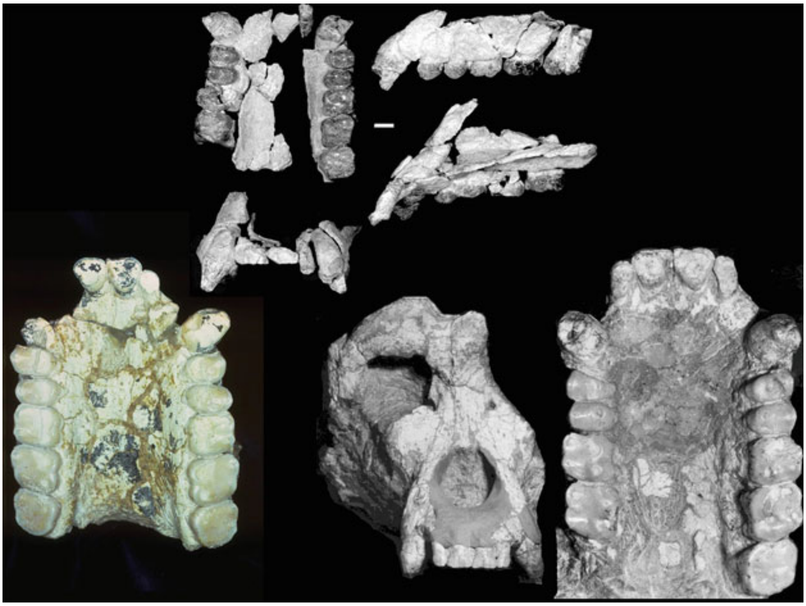


Plate 19 *Ouranopithecus* and "*Ouranopithecus*" *turkae*. *Top*, palatal, anterior, lateral and medial views of "*Ouranopithecus*" *turkae* (CO-205). *Bottom*, from *left* to *right*, RPL 128 and two views of ZIR 1

and the new nomen *Ouranopithecus* (see chapter "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3) was proposed (Bonis and Melentis 1977; Plate 19).

Ouranopithecus is a large hominid, the approximate size of a large male chimpanzee or female gorilla, whose morphology is similar to that of other dryopithecins but with a much more robust masticatory adaptation (Begun and Kordos 1997). *Ouranopithecus* has a palate that is similar to other dryopithecins in the degree and pattern of overlap of the maxilla and premaxilla (Bonis and Melentis 1987; Begun and Kordos 1997). The morphology of the nasoalveolar clivus is also similar to dryopithecins and extant hominines. The nasal aperture is broad at its base, the interorbital space is broad, and the orbits are rectangular. The zygomatic roots arise relatively low and anteriorly on the maxilla, which is interpreted as a homoplasy with Early Miocene taxa, as a similar condition is also found in robust australopithecines that share with *Ouranopithecus* a very robust masticatory apparatus (Begun and Kordos 1997; Begun 2007). The glabella is projecting, and like *Hispanopithecus* and *Rudapithecus*, it is continuous with subtle tori above each orbit. The frontal squama is concave above glabella, as in *Hispanopithecus*, but this is somewhat exaggerated by damage. Dentally, *Ouranopithecus* is similar to dryopithecins and other hominids in tooth proportions and overall dental morphology. It differs from dryopithecins in having hyperthick occlusal enamel, molars with broad cusps and flat basins, mesiodistally longer incisors, and relatively low-crowned male upper canines. The mandibles are also more robust than in other dryopithecins and have strongly reinforced symphyses. The female mandibles tend to be more robust (or shallower) than the male mandibles. One mandible preserves the condylar process, which is large and strongly convex anteroposteriorly. *Ouranopithecus* is also known from two unpublished phalanges.

In many publications, summarized in Bonis and Koufos (1997), it has been argued that *Ouranopithecus* is a hominin (specifically related to humans), mainly on the basis of canine reduction and masticatory robusticity. However, these features occur repeatedly during hominoid evolution. *Ouranopithecus* is most parsimoniously interpreted as a terminal member of the dryopithecin clade, with a number of craniodental specializations related to an increase in masticatory robusticity (Begun and Kordos 1997; Begun 2001, 2002, 2007, 2009). The large jaws and teeth and hyperthick enamel, as well as microwear studies, suggest an ability to exploit hard and/or tough fruits, nuts, and other dietary resources (Kay 1981; Ungar 1996; Bonis and Koufos 1997; Kay and Ungar 1997).

Graecopithecus

Another taxon, *Graecopithecus* (von Koenigswald 1972), is also known from Greece but from a much younger locality over 200 km from the *Ouranopithecus* localities. It is similar to *Ouranopithecus*, and some have suggested that the two samples belong to the same genus, which would be called *Graecopithecus*, since this nomen has priority (Martin and Andrews 1984). In my view, the generic distinction is warranted. *Graecopithecus*, known only from a poorly preserved mandible with a fragmentary M_1, a much worn M_2, and root fragments, is similar to *Ouranopithecus* in apparently having thick occlusal enamel. However, it is the overall size of female *Ouranopithecus* but has an M_2 bigger than some male *Ouranopithecus*, and the M_2 is actually broader than the mandibular corpus at the level of the M_2. The symphysis is more vertical and the M_1 is relatively small (Begun 2002, 2009). *Graecopithecus* is morphologically distinguishable from *Ouranopithecus*, much younger in age, and geographically distant from *Ouranopithecus* localities.

There are two other samples of Late Miocene hominines that have affinities with *Ouranopithecus*. Güleç et al. (2007) described a new species of *Ouranopithecus*, *O. turkae*, based on a large maxilla recovered from the site of Çorakyerler, in Central Anatolia. The site is unique for Eurasian Late Miocene apes in being an open habitat and being young in age (about 8–8.5 Ma). Only *Oreopithecus* in Europe and *Lufengpithecus* in Asia are younger. Having studied the maxilla from Çorakyerler in detail, it is my view that it represents a new genus of hominine (Sevim et al. 2001; Begun 2009; Begun et al. 2012). It is much larger than *Ouranopithecus*, the maxilla fitting comfortably on the mandible of *Indopithecus*, and the anterior dental morphology is quite distinct. However, until more recently recovered specimens are described, I refrain from naming a new genus.

The other sample of Late Miocene hominine that may be attributed to *Ouranopithecus* is the isolated P4 from the site of Azmaka, near Chirpan, Bulgaria (Spassov et al. 2012). The site may be as late as 7 Ma, but only one P4 is known. The specimen is clearly a hominid, and more closely resembles thickly enameled taxa, but its precise affinities remain to be determined.

The greater significance of these two samples from Bulgaria and Turkey are not their taxonomic or phylogenetic affinities, but their location in geographic and temporal space. Both are much later than some have predicted for Miocene apes in Europe, and both are associated with paleoecological settings that some have said excludes the presence of apes (Bernor et al. 2004; Bernor 2007). There are many problems with the naïve preconception that hominines could not have dispersed between Eurasia and Africa in the Late Miocene (see Begun et al. 2012 for a detailed critique). We now know that Late Miocene hominines lived in much drier conditions than previously supposed, and we also know that even without these adaptations, ample evidence exists for forest corridors and refugia in southeastern Europe and North Africa that could have allowed forest-adapted taxa to disperse between the two continents (Begun et al. 2012) The presence of hominines from Çorakyerler and Azmaka demonstrate that it is unwise to exclude a priori an ecological association resulting from the wondrous and unpredictable interaction of natural selection, anatomy, behavior, and ecology.

Paleobiology of the Dryopithecins

Most dryopithecins display dental morphological characters that are very similar to extant *Pan* and suggest a soft fruit diet (Begun 1994a). Microwear analyses support this assessment (Kay and Ungar 1997). The dryopithecin gnathic is gracile compared to many other Late Miocene hominids (less robust mandibles, thinner occlusal enamel, smaller attachment sites for the muscles of mastication), which is both consistent with a soft fruit diet and more similar to extant African apes, *Pan* in particular. Postcranially, *Hispanopithecus* and *Rudapithecus* are unambiguously suspensory, but they do lack a few synapomorphies, particularly of the extremities, which characterize all extant hominids. These have to do mainly with the robusticity of the bones of the carpus and tarsus, which may be attributable to a “red queen” phenomenon, as in the case of the progressive development of shearing quotients during the course of hominoid evolution (Kay and Ungar 1997). In the fossil record of many mammals, there is evidence of a shift toward a certain adaptation (folivory, frugivory, suspension, climbing, bipedalism, etc.) that becomes increasingly refined in individual lineages descended from the common ancestor initially expressing the behavior. In order to remain competitive, the descendants must, in essence, run to stay in the same place, as increasingly efficient versions of the same adaptation appear independently (van Valen 1973). *Rudapithecus* and *Hispanopithecus* were arboreal, suspensory, soft fruit frugivores with a dentition similar to *Pan*, living in seasonal subtropical forests but probably capable of exploiting a variety of resources, possibly including meat (Kordos and Begun 2002).

The exception to this general pattern among the dryopithecins is *Ouranopithecus*, which was a hard/tough object feeder. While the postcrania have not been described in *Ouranopithecus*, it has been suggested that it was probably more terrestrial than other dryopithecins, given its diet and habitat, which was more open country than any other dryopithecin (Bonis and Koufos 1994). However, a definitive answer to the question of the positional behavior of *Ouranopithecus* must await analysis of the phalanges.

Oreopithecus

The other European Miocene hominoid discovered and described during the nineteenth century is the highly unusual *Oreopithecus* (Gervais 1872). Over the years, *Oreopithecus* has been called a pig, prosimian, monkey, and ape, the last being the attribution most researchers agree on today (Harrison and Rook 1997; Moyà-Solà and Köhler 1997; Begun 2002). *Oreopithecus* is younger than other Late Miocene European hominoids and is known from about 6 to 7 Ma localities in Italy. At the time, most of the Italian peninsula was separated from the rest of Europe by the sea, as is today the Italian island of Sardinia, where one *Oreopithecus* locality is found. In the Late Miocene, all *Oreopithecus* localities were insular, and the faunas associated with them are unique and difficult to compare to continental European faunas (Harrison and Rook 1997). *Oreopithecus* is a product of its insular environment as well and is characterized by many unique adaptations that make it difficult to understand its relations to other hominoids.

In its craniodental morphology, *Oreopithecus* is similar to dryopithecins and African apes in having apparently thin enamel, but otherwise the morphology of the teeth is quite unique. Like other hominids, *Oreopithecus* has compressed canines, reduced premolar cusp heteromorphy, and reduced or absent molar cingula. However, the incisors are small and low crowned; the P_4 has a primitive-looking low talonid compared to the trigonid; the postcanine dentition has tall, isolated cusps; and the lower molars have a unique occlusal morphology with a centroconid connected to the four principal cusps by a well-developed system of crests. The upper molars are also strongly “cristodont,” which makes them appear similar to the lower molars, superficially resembling the condition of upper and lower molar bilophodonty in Old World monkeys.

The mandible is strongly built with some specimens being quite robust transversely and others deeper. The ramus is expansive to accommodate large temporalis and masseter muscles, which is also evidenced by the prominent temporal crests and pronounced postorbital constriction. The face is badly damaged but appears to have had a short and relatively gracile premaxilla, which is consistent with the small incisors. The brain case is also badly damaged but was clearly small, housing a much smaller brain than great apes of comparable body mass (Harrison 1989; Begun and Kordos 2004). Like *Sivapithecus* and non-hominids, the articular and temporal portions of the temporal bone are not fused, but like hominids the subarcuate fossae are small. The ectocranial crests are very strongly developed, while the frontal is comparatively smooth, without tori, and the postorbital constriction is marked.

The most impressive aspect of *Oreopithecus* is its postcranium. A remarkably complete but crushed skeleton along with many other isolated postcranial elements is known from *Oreopithecus*. The axial skeleton (rib cage and trunk) is hominoid-like in its short lower back and broad thorax, and the pelvis is also comparatively short and broad, as in hominids. The forelimbs are very elongated compared with the hindlimbs, the glenoid fossa of the scapula is deep, and the elbow has all the typical hominoid features described previously. The femur is short and robust with a large head, and the knee joint indicates mobility in several planes. The hand is long but narrow, and the foot is comparatively short, though in both the hand and foot, the digits are long and curved. The carpals and tarsals are primitive hominoid-like in being transversely gracile compared to their length. They more closely resemble the carpal and tarsal bones of *Proconsul* than those of hominids.

Oreopithecus combines primitive and derived hominoid characters that ironically make it extremely difficult to place phylogenetically, despite its relatively complete preservation. Harrison and Rook (1997) consider *Oreopithecus* to be a stem hominid closely related to the dryopithecins. Moyà-Solà and Köhler (1997); Moyà-Solà et al. (1999) interpret both the dryopithecins and *Oreopithecus* to be stem pongines (see chapter "▶ Defining Hominidae," Vol. 3), and they have also concluded that *Oreopithecus* was an arboreal biped with a well-developed precision grip. However, these conclusions are based in part on an erroneous reconstruction of the hand of *Oreopithecus* (Susman 2004 and personal observations) and a very unlikely reconstruction of the foot (Köhler and Moyà-Solà 1997 and personal observations). Rook et al. (1999) interpret CT scans of the innominate of *Oreopithecus* to imply a remodeling of bone consistent with bipedalism, but alternative interpretations are in my view more likely (Wunderlich et al. 1999). Overall, the overwhelming signal from the postcranium of *Oreopithecus* is of a suspensory arboreal adaptation. The long, curved phalanges are unambiguous indicators of suspension and incompatible with either bipedalism or a precision grip.

Though some have interpreted aspects of the cranial morphology of *Oreopithecus* to have resulted from neoteny leading to a superficially primitive morphology (Moyà-Solà et al. 1997; Alba et al. 2001), it is very difficult to identify heterochrony in fossil taxa (Rice 1997), and the much more straightforward interpretation is that *Oreopithecus* does in fact retain a number of primitive characters not found in other Late Miocene or extant hominids (Harrison 1986; Harrison and Rook 1997; Begun 2002). These include a short, gracile premaxilla, large incisive foramen, low position of the zygomatic root, small brain, a number of features of the basicranium, and several postcranial characters (gracile phalanges; transversely small carpals; short, relatively gracile tarsals; etc.). It is very unlikely that a single growth process resulting from selection for bipedalism and an omnivorous diet, as suggested by Alba et al. (2001), would have produced such a diversity of consistently primitive characters throughout the skeleton.

The extraordinary morphology of the cranium and dentition of *Oreopithecus* are probably related to a specialized folivorous adaptation. *Oreopithecus* molars have the highest shearing quotients of any hominoid, which is consistent with a high-fiber diet (Kay and Ungar 1997). The exceptionally developed chewing muscles of *Oreopithecus*, its robust mandibles, and even the small size of its brain are all consistent with a folivorous diet requiring high-bite forces but relatively little planning or "extractive foraging" (Begun and Kordos 2004).

Late Miocene East African Hominines?

At the same time that Late Miocene apes are flourishing in Eurasia, two taxa, recognized from small samples, are known from East Africa. *Chororapithecus* is recognized from a small number of isolated teeth from Ethiopia dated to between about 10 and 10.5 Ma

(Suwa et al. 2007). They accept, based on molecular clock evidence, that the divergence of *Pongo* and the African apes and humans occurred at about 20 Ma, that for *Gorilla* at about 12 Ma, and that for *Pan* and humans at about 9 Ma. These divergence dates are of course the subject of much discussion. These authors cautiously assign *Chororapithecus* to the gorilla clade, suggesting that *Chororapithecus* represents an early gorilla. The main line of evidence is a crest revealed by CT scans on the dentine surface of one of the molars, which the authors suggest is an indication of an adaptation to shearing, characteristic of gorillas. However, the ridge in question is only present on the dentine surface and not the surface that would have been in contact with food. Therefore, even if this dentine crest is homologous with a ridge on the teeth of gorillas, it is very doubtful that it represents an adaptation to shearing, since it could never have encountered a single fiber of food (being buried under the enamel cap). At best this crest, if found to be homologous with a crest on the enamel surface of a gorilla tooth, would be considered an exaptation and not evidence of selection for a gorilla-like mode of adaptation suggested by Suwa et al. (2007).

The sample of *Chororapithecus* is fragmentary, and frankly, if found anywhere outside of Ethiopia, it would be considered inadequate to support any particular phylogenetic hypothesis. It is in the right place the right time, according to some scenarios, but when examined in detail, it fails to demonstrate the presence of a gorilla at 10 Ma, or even a hominine. The fragmentary nature of these specimens does not allow for a definitive assignment of *Chororapithecus* to a hominid clade. I would not exclude the possibility that it is a late surviving *Proconsul*.

Another collection of fossils from East Africa is *Nakalipithecus*, from Kenya, dated to about 9.8 Ma (Kunimatsu et al. 2007). The sample consists of a fragmentary mandible and some isolated teeth. Sadly, the teeth in the mandible are highly worn, making it difficult to use this most complete specimen to assign this taxon to the sister clade to *Ouranopithecus*, as suggested by the authors. There is, however, a female upper canine that does bear a strong resemblance to *Ouranopithecus* (Kunimatsu et al. 2007). In my view, *Nakalipithecus* is more likely to be a hominine and to be related to Eurasian apes than *Chororapithecus*. Kunimatsu et al. (2007) suggest that *Nakalipithecus*, because its known range is slightly older than the known range of *Ouranopithecus*, might be ancestral to the Greek ape. The time difference between the two samples however is minimal by paleontological standards (9.5 vs. 9.8). *Nakalipithecus* represents the best connection in the Late Miocene between Europe and Africa, but there is no good evidence that *Nakalipithecus* is ancestral to *Ouranopithecus*. Given the close ages of both samples, it cannot be said which is ancestral to which. It remains true, however, that the earliest hominines are at least 12.5 Ma from Europe, so that whatever the relationship is between *Nakalipithecus* and *Ouranopithecus*, the Eurasian taxa came first.

Late Miocene Hominid Extinctions and Dispersals

Hominids first appear in the Middle Miocene of Eurasia and quickly radiate, but between about 10 and 9 Ma they begin to disappear. The view presented here is that the hominids from western Eurasia are hominines, and those in the east are pongines (Begun 2004, although see above for an alternative interpretation). Descendants of each subfamily eventually disperse south of the Tropic of Cancer as other taxa become extinct in Eurasia (Begun et al. 1997, 2012; Begun 2001, 2004). This view has been supported by genetic evidence (Stewart and Disotell 1998) and criticized based on differing interpretations of the fossil record. For example, it has been noted that Africa is a more likely place for the origin of the Hominidae and the Homininae, presumably because African apes still live there and because it is said to be poorly sampled, especially in the Late Miocene. The fossils that would support this interpretation remain to be discovered. In fact, many Late Miocene localities are known from Africa, a number with paleoecological indications of forested settings (Begun 2001, 2004; Begun et al. 2012), yet no hominines have ever been identified in Africa dating between *Kenyapithecus* and *Sahelanthropus* apart from *Chororapithecus* and *Nakalipithecus*, which, as noted, may be hominines but are much younger than the earliest European hominines. *Samburupithecus* is also present in this time period, but it is even more primitive and less likely to be a hominine than *Chororapithecus* and *Nakalipithecus*. *Samburupithecus* retains many primitive dental and maxillary characters (Begun 2001). Isolated teeth from Ngorora have been described as having affinities primarily with the Proconsuloidea or Middle Miocene East African hominoids (e.g., *Equatorius*) (Hill and Ward 1988; Begun 2001; Hill 2002). Pickford and Senut (2005) have recently reported teeth from Ngorora and Lukeino described as chimpanzee and gorilla-like, but in my view, the older teeth cannot be distinguished from others with affinities to the Proconsuloidea, and the younger teeth are probably from *Orrorin* (see chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3), known from the same locality (Lukeino) (Senut et al. 2001). Most importantly, an African origin of the hominines to the exclusion of the European taxa fails to explain the widespread pattern, from Spain to Hungary, of morphology associating Eurasian apes with those from Africa. To deny a European origin of the Homininae based on the evidence to date is to evoke ad hoc hypotheses of convergence or homoplasy to explain away the documented similarities between dryopithecins and crown hominines. One can choose not to believe a hypothesis because of an a priori expectation that evidence disproving it will eventually be found (e.g., Bernor 2007), but in my view, this is not an acceptable approach to science.

Hominids appear to have moved south from Eurasia in response to global climate changes that produced more seasonal conditions in Eurasia toward the end of the Miocene (Quade et al. 1989; Leakey et al. 1996; Cerling et al. 1997; Begun 2001, 2004, 2009; Fortelius et al. 2006; Agustí 2007; Agustí et al. 2003; Nargolwalla 2009) (see Begun et al. (2012) for a comprehensive review of the evidence of faunal dynamics and climate change in the Late Miocene). Much evidence exists for climate change throughout much of Eurasia in the Late Miocene, which led to the development of more seasonal conditions. This culminates in the Messinian Salinity Crisis that led to the desiccation of the Mediterranean basin at the end of the Miocene (Hsü et al. 1973; Clauzon et al. 1996; Krijgsman et al. 1999). Other consequences include the development of Asian monsoons, desertification in North Africa, the early phases of Neogene polar ice cap expansion, and the expansion of North American grasslands (Garcés et al. 1997; Hoorn et al. 2000; Zhisheng et al. 2001; Griffin 2002; Guo et al. 2002; Janis et al. 2002; Liu and Yin 2002; Wilson et al. 2002). In both Europe and Asia, subtropical forests retreat and are increasingly replaced by more open-country grasslands and steppes (Bernor et al. 1979; Bernor 1983; Fortelius et al. 1996; Cerling et al. 1997; Bonis et al. 1999; Magyar et al. 1999; Solounias et al. 1999; Fortelius and Hokkanen 2001). In some places, forests persisted and elsewhere more severe changes occurred, creating a number of refugia, some of which continued to host hominids well into the period of climatic deterioration. This is the case for the *Oreopithecus* localities of Tuscany and Sardinia (Harrison and Rook 1997). Other well-known localities, such as Dorn-Dürkheim in Germany, retain a strongly forested character, though they lack hominoids (Franzen 1997; Franzen and Storch 1999).

There is a gradient of extinctions of forest forms from west to east corresponding to the gradient of appearance of more open-country faunas from east to west (Bernor et al. 1979; Fortelius et al. 1996, 2001; Begun 2001, 2004). Between about 12 and 10 Ma, *Dryopithecus* disappears from localities in Europe, becoming very rare by 9.5 Ma in Spain and Germany. This wave of extinctions ends coincident with an important faunal event in Western Europe known as the mid-vallesian crisis, when a major turnover of terrestrial faunas leads to the widespread extinction of local taxa generally attributed to the development of more open conditions (Moyà-Solà and Agustí 1990; Fortelius et al. 1996). The youngest specimens possibly attributable to *Dryopithecus* are the most easterly, currently assigned to *Udabnopithecus* from the 8 to 8.5 Ma locality of Udabno in Georgia (Gabunia et al. 2001).

In the eastern Mediterranean, hominids persist to the end of this time. *Ouranopithecus* in Greece is mainly known from the end of the hominid presence in Europe and may be a terminal taxon of the *Dryopithecus* clade (Begun and Kordos 1997). In Anatolia, at the eastern edge of the faunal province that includes Greece and the eastern Mediterranean (the Greco-Iranian province (de Bonis et al. 1999)), a very large hominid resembling *Ouranopithecus* may be as young as 7–8 Ma in age (Sevim et al. 2001). At this time, forest taxa are increasingly replaced by more open-country forms. This is true of virtually all mammalian orders. Among the primates, hominoids decline and cercopithecoids are on the increase (Andrews et al. 1996). Grazing ungulates and grassland or dry ecology-adapted micromammals also become more common (Fortelius et al. 1996; Agustí et al. 1999; de Bonis et al. 1999; Solounias et al. 1999; Agustí 2007).

The dispersal of Late Miocene faunas between Eurasia and Africa is complex and includes both open and more forest-adapted taxa. Among the more open-country taxa, horses disperse from North America to the Old World, and modern bovids and giraffids appear to have dispersed from Europe to Africa (Dawson 1999; Made 1999; Solounias et al. 1999; Agustí et al. 2001). Among the more close setting mammals, hippos move from Africa to Europe, and pigs of varying ecological preferences move from Asia to Europe and Africa (Fortelius et al. 1996; Made 1999). Small carnivores (mustelids, felids, and viverrids), larger carnivores (ursids, hyaenids) porcupines, rabbits, and chalicotheres, most of which also prefer more closed settings, also disperse from Eurasia to Africa (Leakey et al. 1996; Ginsburg 1999; Heissig 1999; Made 1999; Winkler 2002).

Many of these dispersals involved forest or wetter ecology taxa (hippos, some suids, primates, carnivores, rodents, and chalicotheres), which is consistent with the evidence of climate change at that time. There is ample time between 10 and 7 Ma for the dispersal of forest-adapted taxa between Eurasia and Africa before the onset of the severe dry spell that culminates in the Messinian, including evidence of forest corridors and refugia well into the Late Miocene in the Balkans and North Africa (Pickford et al. 2006; Begun et al. 2012). Taxa disperse south into Africa as conditions continue to deteriorate leading to the Messinian crisis, among them probably the ancestors of the African apes and humans. This scenario has hominid ancestors leave Africa in the Early Miocene and return as hominines in the Late Miocene, but this is precisely what seems to have occurred in several mammalian lineages, including those represented by Late Miocene African species of *Orycteropus* (aardvark), several small carnivores, the hippo *Hexaprotodon*, and possibly the proboscideans *Anancus*, *Deinotherium*, and *Choerolophodon* (Leakey et al. 1996; Ginsburg 1999; Heissig 1999; Made 1999; Boisserie et al. 2003; Werdelin 2003; Begun and Nargolwalla 2004).

Conclusion

The Miocene epoch witnesses several adaptive radiations of hominoids and hominoid-like primates. It was indeed the golden age of the Hominoidea. Many catarrhines appear in East Africa in the Early Miocene, some of which are surely related to living hominoids. A few of the basic attributes of the Hominoidea appear at this time, including the absence of a tail, somewhat extended life history, and a hylobatid level of encephalization, and hints of powerful hand and foot grips and a propensity for more vertical climbing. Among the diversity of Early Miocene Hominidea, a group emerged that may have had an adaptation to a diet dependent on more embedded resources, leading to a dispersal into Eurasia. Once there, hominoids flourish and expand, splitting into eastern and western clades that led to extant hominids (hominines in the west and pongines in the east) and an early southern clade that becomes extinct. Early in the Late Miocene, the hominid radiation in Eurasia began to dwindle, with the earliest extinctions occurring in the west and progressing eastward. Hominids and many other mammals experienced extinction events at this time, and many clades of Eurasian mammals also dispersed south, probably as a result of major global climatic events. Western Eurasian hominines dispersed into Africa, leading to the evolution of the African apes and humans, and eastern pongines dispersed into Southeast Asia, leading to the appearance of the *Pongo* clade. Shortly after their dispersal into Africa, hominines diverged into their respective clades, probably relatively quickly. Gorillas remain the most conservative in many respects, though they achieve some of the largest body masses in any primate and specialize in their ability to exploit high-fiber keystone resources.

Chimpanzees and humans diverged, possibly within a million years of the emergence of the gorilla clade, the chimp clade remaining relatively conservative and the human clade experiencing much more rapid and dramatic evolutionary changes. Human ancestors retain the imprint of their Eurasian and African ape ancestors and were very probably similar to extant African apes, particularly chimpanzees, that is, the fossil record of hominoid evolution suggests that humans evolved from a knuckle-walking, forest-dwelling soft fruit frugivore/omnivore, not a chimpanzee in the modern sense, but more chimp-like than anything else nonetheless. The details of the evolutionary events leading to the origin of the individual lineages of the Homininae remain to be worked out, a process hampered in part by a poor fossil record that, for example, includes almost no fossil relative of gorillas or chimpanzees (but see McBrearty and Jablonski 2005).

Cross-References

▶ Defining Hominidae
▶ Dental Adaptations of African Apes
▶ Estimation of Basic Life History Data of Fossil Hominoids
▶ Great Ape Social Systems
▶ Hominoid Cranial Diversity and Adaptation
▶ Origin of Bipedal Locomotion
▶ Postcranial and Locomotor Adaptations of Hominoids
▶ Potential Hominoid Ancestors for Hominidae
▶ Role of Environmental Stimuli in Hominid Origins
▶ The Hunting Behavior and Carnivory of Wild Chimpanzees
▶ The Miocene Hominoids and the Earliest Putative Hominids
▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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The Biotic Environments of the Late Miocene Hominoids

Jordi Agustí

Contents

Abstract

The habitat of the Middle and Late Miocene hominoids from western Europe, like *Dryopithecus*, was characterized by the prevalence of subtropical conditions. As a consequence, those environments were mainly dominated by fruit eaters and browsers, including a large variety of suids, cervids, rhinos, chalicotheres, and proboscideans. In contrast, in large parts of Eurasia, from eastern Europe (Greek-Iranian province) and northern Africa to China, the Middle Miocene climatic crisis led to the development of a xerophilous woodland, dominated by bovids, giraffids, and pursuit carnivores. At first, the worldwide dispersal of the hipparionine horses changed this scenario very little. However, at 9.6 Ma, a significant event, the Vallesian Crisis, led to the extinction

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J. Agustí (✉)
ICREA-Institute of Human Paleoecology, Universitat Rovira i Virgili, Tarragona, Spain
e-mail: jagusti.ballester@gmail.com; jordi.agusti@icrea.es

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of most of the fruit eaters that had prevailed in the Middle Miocene European faunas. Hominoids persisted for a time in the Tusco-Sardinian Island and in the low latitudes of southwestern Asia. The worldwide spread of grasses between 8 and 7 Ma led to the final extinction of those hominoids. Hominoid evolution continued in eastern and southeastern Africa, in a habitat that strongly resembles that of the Greek-Iranian province.

Introduction

The Late Miocene, that is, the timespan between 11.6 and 5 Ma, is a crucial period in understanding the configuration of our present world. This is the time when the persisting laurophyllous evergreen woodlands (also called *laurisilvas*), which had spread over large parts of the Old World during most of the Miocene, were replaced by drier and more seasonal ecosystems, including savannas and steppes. It has been argued that the spread of this kind of environment may have played a key role in hominid evolution, by enhancing the appearance of new locomotor innovations, such as bipedalism (Lovejoy 1980; Coppens 1983). However, this change toward increasing dryness and seasonality was not a sudden one. Instead, this general trend appears to have been punctuated by a number of faunal and environmental events, which predated the onset of glacial-interglacial dynamics in the Northern Hemisphere. Significant physiographic and tectonic events appear also associated with this biotic turnover, such as the uplift of the Himalayas and the Tibetan Plateau, the final closure of the Atlantic-Indian seaway throughout the Mediterranean, and the desiccation of the Paratethys and Mediterranean seas. These paleogeographic events severely affected the continent-ocean interplay system, leading to changes in the overall circulation pattern, enhancement of the monsoonal dynamics, and the development of the first Arctic glacials.

The Middle Miocene Environmental Background: The World of *Dryopithecus*

Despite the climatic crisis that affected the Early Miocene terrestrial ecosystems, the last part of the Middle Miocene was characterized by very favorable biotic conditions in parts of western Eurasia, specially in western and central Europe (Agustí and Antón 2002; Fortelius et al. 2003). The faunal associations from these regions were characterized by high mammalian diversity levels, with a high amount of large- to medium-sized browsers, together with several medium-sized carnivores. At the top of the large browser guild were the proboscideans, represented by the large gomphotheres of the genus *Tetralophodon* and the deinotheres of the genus *Deinotherium*. *Tetralophodon* was a late immigrant in the Middle Miocene terrestrial ecosystems and replaced the once worldwide gomphotheres of the genus *Gomphotherium*. *Tetralophodon* was a large proboscidean which had more hypsodont teeth than the earlier gomphotheres. Moreover, its skull, although still bearing four tusks, was shorter and more elephant-like, with a pair of long, straight tusks in the maxilla and a small pair of tusks at the end of the mandible. In contrast, *Deinotherium* represents a completely different kind of proboscidean. Members of this group had only two strong tusks, not placed in the upper jaw but at the end of the mandible. Moreover, this lower pair of tusks was recurved downward. The molars were very simple, formed of two cutting ridges, interpreted as an adaptation to browsing leaves and tough vegetation.

Another main component of the large browser community was the chalicotheres, a group of bizarre perissodactyls distantly related to horses that prolonged the trend observed in other ungulates to enlarge the forelimbs relative to the hind limbs. This trend reached an extreme in some Miocene representatives, such as *Chalicotherium*, which developed gorilla-like limb proportions, with very long forelimbs and short hind limbs. The chalicotheres bore claws at the end of their arms, instead of the typical hoofs of the odd-toed ungulates. These enabled them to grasp small branches and leaves with the help of their forefeet. These large perissodactyls were probably capable of standing on their hind limbs and using their forelimbs as “hands” to reach the higher vegetational levels.

However, the most diversified group of large browsers were the rhinoceroses, represented by several different forms, such as *Brachypotherium*, *Hoploaceratherium*, *Alicornops*, or *Lartetotherium*. *Brachypotherium* was a large teleoceratine with hypsodont teeth, short legs, and hippolike body proportions, which probably had a semiaquatic lifestyle. Another group was the aceratherine rhinos, represented by the genera *Hoploaceratherium* and *Alicornops*. *Hoploaceratherium tetradactylum* was a medium-sized acerathere with long limbs and slender body proportions. As in most aceratherines, the characteristic horns were highly reduced (only a small one was present). In contrast, they displayed very big lower incisors, which were larger in the males. *Alicornops simorrense* was a small acerathere with short, tridactyl legs and strongly curved lower incisors (although, as in *Hoploaceratherium*, a small horn was present). The rhinocerotines or “modern horned rhinos” were represented by *Lartetotherium* and “*Dicerorhinus*” *steinheimensis*. *Lartetotherium sansaniense* was a cursorial rhino that had a unique, long horn. According to its rather brachydont teeth, its diet must have contained a higher quantity of soft plants and a lower proportion of wooden parts of shrubs than in the case of the aceratherine rhinos (Heissig 1989).

Represented only by the genus, *Anchitherium*, the equids were also significant elements of the Miocene ecosystems. *Anchitherium* was a member of the group of North American horses that experienced a significant evolutionary radiation during the Oligocene. This medium-sized anchitherine, about 1 m or less at the withers, crossed the Bering area in the Early Miocene and rapidly dispersed over the whole of Eurasia, from China to Spain. They bore low-crowned (brachydont), lophodont teeth adapted to browsing soft leaves. Their limbs were also adapted to locomotion on soft substrates, still retaining two lateral, fully functional toes.

The undergrowth of the Middle Miocene laurisilva was populated by a wide array of suids, which included hyotherines (*Hyotherium*), peccary-like suids (*Taucanamo*, *Albanohyus*), tetraconodontines (*Conohyus* and its offshoot

Parachleuastochoerus), and listriodontines (*Listriodon*). *Taucanamo* was a small peccary-like pig (about 12 kg), which developed lophodont teeth and large, elongated premolars. Its dental morphology, with high cusps and variable lophodonty, resembles that of some cercopithecoid primates and tragulids, being probably related to a browsing regime in a forest biome. *Albanohyus* was a small peccary-like suid also found at Fort Ternan that resembled *Taucanamo* but had smaller, shorter premolars. *Listriodon* was a fully lophodont, browsing listriodontine, which dispersed over the whole of Eurasia, from China to the Iberian peninsula throughout eastern and central Europe (Made 1996). Analysis of microwear in *Listriodon* has shown a rather uniform diet with a smaller minerogenic component, which indicates a variation from the typical rooting behavior of generalized suids and a specialization in the browsing of vegetation. Lengthening of distal limb segments might indicate that these listriodontines preferred more open habitats. Together with the listriodontines, a new subfamily of suids, the tetraconodontines, became the dominant suiforms in the circum-Mediterranean area (including five genera: *Conohyus*, *Parachleuastochoerus*, *Sivachoerus*, *Notochoerus*, and the African *Nyanzachoerus*). The tetraconodonts bore thick-enameled cheek teeth and conical premolars with hyena-like wear, which probably indicates a diet based on hard food items such as seeds. A trend toward reducing size is present in this group during the Middle Miocene, from the 70 kg of the medium-sized *Conohyus* to the 40 kg of the small *Parachleuastochoerus*. Later on, at the end of the Middle Miocene, the suid diversity increased again with the appearance of the first representatives of modern suids (*Propotamochoerus*). *Propotamochoerus* was a large suid (about 120 kg), which probably evolved in southern Asia from a hyotherine pig during the Middle Miocene and subsequently extended its range westward into southwestern Asia and Europe. It is the first recognizable member of all modern swines. The molars of this group show a trend toward the proliferation of several minor cusps, concomitant with loss of cusp identity. This peculiar dental evolution resembles some bears and indicates a further adaptation to omnivory.

Other significant members of the medium-sized browser community were the deer or cervids, represented by a number of genera such as *Heteroprox*, *Dicrocerus*, and *Euprox*. According to their limb proportions and low-crowned (brachydont) dentitions, most of these archaic deer were semiaquatic browsers that lived in closed forests in humid conditions (Köhler 1993). They still displayed rather simple, two-pronged antlers, although in some cases like *Euprox*, there was a differentiation between a principal, posterior prong and a secondary, smaller anterior prong. Some of them, like *Dicrocerus* and *Euprox*, showed a burrlike area, indicating for the first time the border between the deciduous and permanent segments of the antlers. Besides cervids, other related taxa, such as the moschid *Micromeryx* and the tragulid *Dorcatherium*, testify to the persistence of very humid conditions in western and central Europe. *Micromeryx* was a very small and slender moschid of less than 5 kg that, as in the case of the living moschids, lacked horns but displayed very prominent canines (in the males). *Micromeryx* probably foraged in the lower vegetation of the closed forest, again living on soft plants and fruits, larvae, and carrion (Köhler 1993). It was a very successful moschid that spread over a wide area covering western and eastern Europe and that persisted until the Late Miocene (Early Turolian). Among these small browsers, other significant elements were the tragulids of the genus *Dorcatherium*. The tragulids or chevrotains are small ruminants that today live close to the water in the closed forests of tropical Africa and east Asia. Like the moschids, they lack any kind of cranial appendages, having in their turn a pair of long canines which are longer in the males. Moreover, they retain a very primitive limb structure, with four well-developed toes on each foot (the two central metapodials are not yet fused in the cannon bone). The recent relatives of *Dorcatherium*, the chevrotains *Hyemoschus aquaticus* and *Tragulus meminna*, live in dense tropical forests close to rivers or water courses, which act as a refuge in the case of sudden attack by predators. *Dorcatherium* was nearly identical in all aspects to the recent *Hyemoschus* and probably developed a similar lifestyle.

In contrast, the bovids were poorly diversified at this time, mainly represented by *Eotragus*. The first bovids such as *Eotragus* probably originated in Asia, to the south of the Alpine belt. Later, in the Early Miocene, they colonized Europe and Africa simultaneously, their presence in this latter continent having been reported from Gebel Zelten (Libya) and also from Maboko and Ombo (East Africa). *Eotragus* was a small ruminant, the size of the living dik-dik or dwarf antelopes of the tribe Neotragini. The horn cores were short and conical, placed directly over the orbits. The teeth were brachydont, indicating a diet based on soft plants, fruits, larvae, insects, or even carrion. Their limb proportions were primitive, close to those of a cervid. They probably occupied a closed, wooded habitat where they probably ducked under the undergrowth (Köhler 1993).

At the opposite extreme, the small herbivore guild was extensively represented by a variety of rodents, including several species of hamsters (cricetids), dormice (glirids), eomyids, squirrels (sciurids), and beavers (castorids). The laurophyllous forests at this time were populated by a variety of flying rodents, such as flying squirrels of different sizes (from the large *Albanensia* to the small *Blackia*) and, probably, the eomyids *Eomyops* and *Keramidomys*. But other groups of small rodents, such as some glirids of the genus *Glirulus*, also developed "flying" forms with a patagium. This is very unusual among dormice and provides a strong indication of the persistence of closed forests at that time in western and central Europe. Another indication of the persistence of humid conditions in this part of the Old World is the frequent discovery of beavers in these faunas. One of them, *Chalicomys*, strongly resembled in size and morphology of the recent *Castor fiber* and, like the living form, was probably highly dependent on permanent rivers. A second smaller beaver, *Trogontherium*, is widely present at this time and was probably associated with more unstable environments.

Among the carnivores, the large predator guild was represented by amphicyonids and nimravids. The amphicyonids, or "bear dogs," resembled canids in their dentition but developed ursidlike characteristics such as very large size and robust canines (with double cutting edges in the case of the upper ones). The heavy carnassials with horizontal abrasion were probably used for bone crushing, an interpretation supported by the high sagittal crests in the skull, which housed a powerful musculature probably used for breaking bones. All these adaptations suggest that the amphicyons were probably occasional scavengers, at a time when truly scavenging specialists were still absent. However, despite these scavenging adaptations, the body plan of the amphicyonids indicates active hunting. They were probably active and agile predators practicing the solitary stalk-pounce hunting mode of recent felids and bears. Their long tails were probably used to balance the pounce, as in the case of the modern felids (Viranta 1996). The Middle Miocene records the first appearance of one of the most successful amphicyonid species in the Miocene, *Amphicyon major* (starting from Neudorf-Spalte and several localities in Spain, France, Germany, Czechia, Turkey). This was a large form, attaining the size of a lion. *Amphicyon major* had a long skull, with an elongated snout and relatively long and massive canines. The general limb proportions were similar to those of a bear, with short metapodials. Besides bearlike forms, like *Amphicyon major*, the amphicyonids also produced at this time hypercarnivorous forms such as *Thaumastocyon* and *Agnotherium*. Both were medium- to large-sized amphicyonids with a cursorial body plan that probably indicates pursuit hunting habits.

However, the typical hypercarnivorous predators of this time were the nimravids, a family of carnivores that developed felidlike, sabertooth adaptations. At the end of Middle Miocene, this family was represented by *Sansanosmilus jourdani*, a large species which reached 80 kg. The true felids were represented at that time by smaller species, all included in the genus *Pseudaelurus*: *P. turnauensis*, *P. lorteti*, and *P. quadridentatus*. The true ursids were represented at this time by two mesocarnivore forms, *Hemicyon* and *Plithocyon*, as well as a typical omnivore form, *Ursavus*. This last genus of small ursids was represented by *U. primaevus* of about 90 kg. The hyenids were represented by slender forms, such as *Protictitherium*, *Plioviverrops*, and *Thalassictis*. Different from the living members of this family, these primitive hyenids were more civetlike generalized carnivores than true scavengers. *Protictitherium* was an archaic insectivore/omnivore form, with very generalized dentition displaying a full set of premolars and molars. The postcranial skeleton suggests a semiarboreal existence and a diet consisting of small mammals, birds, and insects, far removed from the lifestyle of the modern hyenas. *Plioviverrops* was a mongoose-like insectivore/omnivore carnivore, which shows a progressive adaptation to insectivory, as indicated by the reduction of the sectorial portion of the dentition and the increase in the number of high, puncture-crushing cusps on the cheek teeth. Its skeleton was apparently more adapted to a terrestrial lifestyle than *Protictitherium*. *Thalassictis*, represented by the species *T. montadai* and *T. robusta*, was the first member of a hyenid lineage characterized by wolflike meat- and bone-eating habits. They still retained an unspecialized dentition, in some way similar to that of canids, although with a major emphasis on bone eating. The postcranial skeleton indicates terrestrial locomotion but without special adaptations to cursoriality. Unlike *Protictitherium* and *Plioviverrops*, it indicates an adaptation to a more open woodland environment (Wenderlin and Solounias 1991, 1996).

Finally, at the very end of the Middle Miocene, a number of elements of probable African origin entered Eurasia again. This was the case, for instance, for the giraffids of the genus *Palaeotragus*. *Palaeotragus* was a relatively small, slender giraffid of about 250 kg bearing a pair of parallel ossicones standing upright over the orbits. They had long legs and limb proportions resembling those of the living okapi. The structure of the foot indicates that they were probably open-country runners and, perhaps, good jumpers (Köhler 1993). They probably ate soft plants, mainly leaves, which they took hold of by grasping them with their long tongues. Besides *Palaeotragus*, other immigrants at the end of the Middle Miocene were the hominoid dryopithecines of the genera *Pierolapithecus* and *Dryopithecus*, which joined the previously existing pliopithecid anthropoids of the genus *Pliopithecus*. The coexistence of dryopithecids and pliopithecids is probably explained by the different dietary habits. While *Pliopithecus* and other pliopithecids were folivorous primates that settled on sclerophyllous woodlands, the dryopithecids, such as *Dryopithecus*, were frugivorous forms that lived in the canopy of the evergreen laurophyllous forests. In central Europe, the thin-enameled dryopithecids replaced the last thick-enameled hominoids of the genus *Griphopithecus*, which entered this region at the beginning of the Middle Miocene.

The Greek-Iranian Province

While, as we have seen, the Middle Miocene polar cooling and East Antarctic Ice growth did not imply a significant decrease in diversity in the evergreen woodland ecosystems of western and central Europe, its effects were much more severe in middle- to low-latitude terrestrial environments. There was a climatic trend toward cooler winters and decreased summer rainfall. Seasonal, summer drought-adapted sclerophyllous vegetation progressively evolved and spread geographically during the Miocene, replacing the laurophyllous evergreen forests which were adapted to moist, subtropical, and tropical conditions with temperate winters and abundant summer rainfalls (Axelrod 1975). These effects are clearly seen in a wide area to the south of the Paratethys realm, extending from eastern Europe to western Asia. According to Bernor (1984), this region, known as the Greek-Iranian or sub-Paratethyan province, acted as a woodland environmental "hub" for a corridor of open habitats which extended from western North Africa eastward across Arabia into Afghanistan, northwest into the eastern Mediterranean area, and northeast into north China. The Greek-Iranian province records the first evidence of open woodlands through which a number of derived, open-country large mammals, such as hyenids, thick-enameled hominoids, bovids, and giraffids, diversified and dispersed into East Africa. The mammal composition of the Greek-Iranian province was very different from that of the more wooded environments that persisted in most of western and central Europe and approached in some ways that of the recent African savannas. This is why it has often been regarded as a "savanna-mosaic" (Bernor 1984) or "protosavanna" (Harris 1993) chronofauna. But in fact, as demonstrated by several analyses, this eastern biome was closer to an open sclerophyllous woodland than to the extensive grasslands present today in parts of Africa (Eronen et al. 2009; Koufos 2006). Nevertheless, the peculiar biotope that developed in the

Greek-Iranian province acted as the background from which the African savannas evolved during the Plio-Pleistocene (Solounias et al. 1999). They also include a number of genera common to the open-country chronofauna, which dominated the Late Miocene Old World. This evolution has been documented in East Africa, where a similar ecosystem of seasonally adapted, sclerophyllous woodland, with terrestrial hominoids (*Kenyapithecus*), was present in Fort Ternan (Kenya) as early as 14 Ma, in association with the first grasslands in eastern Africa (Dugas and Retallack 1993).

At the taxonomic level, this habitat change in the western European low latitudes involved the rapid adaptive radiation of woodland ruminants (bovids and giraffids). Thus, although the small *Eotragus* persisted and is found to have been widespread throughout Europe, western Asia, and Africa, a new group of larger bovids, the boselaphines, spread at this time, becoming the most successful elements of this family during most of the Miocene. The boselaphines, today represented by the nilgai (*Boselaphus tragocamelus*) from India, began a successful evolutionary radiation in the Middle Miocene, which led to a high generic diversity. *Miotragocerus*, the first boselaphine to appear in Europe, is found from Byelometcheskaya in the Caucasus to Tarazona in central Spain. It was a medium-sized bovid of about 80 kg with strong horn cores that looked very different from those of *Eotragus*. Its teeth were still primitive but with some cementum. The limb bones and foot anatomy indicate that *Miotragocerus* lived in very humid habitats, where it probably fed on soft plants (Köhler 1993). At that time, a second boselaphine bovid in the Greek-Iranian province, *Austroportax*, displayed a quite different aspect. *Austroportax* was a large and surprisingly advanced bovid for its time. It weighed about 300 kg and was supported by short, heavy extremities resembling those of the living buffalos and other modern members of the tribe Bovini. Its foot morphology indicates that it lived in humid and wooded habitats.

A second group of successful bovids that spread at that time over southern Europe and Africa originated from a Middle Miocene Asian form called *Caprotragoides*. Following the Middle Miocene environmental changes, *Caprotragoides* spread over Europe and northern Africa throughout the Greek-Iranian province, leading to *Tethytragus* and *Gentrytragus*, respectively. They were medium-sized bovids of about 30 kg with horn cores curved backward and slightly outward. The teeth morphology indicates a diet based on a great variety of plants. Most of their characters seem to be adaptations to dwelling in open country, but others indicate more wooded preferences. This mosaic of features indicates that *Caprotragoides*, *Tethytragus*, and *Gentrytragus* were probably eurytopic bovids with a high capability of invading very diverse biotopes.

A third group of advanced bovids that spread at this time were the hypsodontines. *Hypsodontus* was a medium to large (about 110 kg) slender and specialized long-legged bovid. It differed from the Boselaphini, *Eotragus*, or *Tethytragus* in its extremely hypsodont cheek teeth, indicating a diet based on grass and tough plants. It attained a broad Old World distribution in the Middle Miocene, from China to India, eastern Europe, and Africa. A second genus related to *Hypsodontus*, *Turcocerus*, was present in Turkey at the same time. *Turcocerus* was a very small bovid with slender, though massive, metapodials. It bore two short conical horns showing a clockwise torsion. The teeth were also very hypsodont and with cement, indicating a diet based on leaves, herbs, and grasses.

A fourth group of advanced bovids that spread in the Middle Miocene were the Antilopini, mainly represented by the gazelles. The first gazelles (*Gazella*) come from the Early Miocene beds of the Chinji zone of Siwaliks and from Majiwa in Kenya (Thomas 1984). According to these data, *Gazella* and other Antilopini could have originated in Africa or the Siwaliks from a form close to *Homoiodorcas* or a related Neotragini. Gazelles dispersed into Europe at this time from their possible Afro-Arabian origins, perhaps taking part in the same dispersal event as *Giraffokeryx* and the kubanochoerus (see below).

Not only gazelles but also the giraffids experienced a wide adaptive radiation in Africa after their dispersal from Asia. One of these giraffids, *Giraffokeryx*, dispersed out of Africa and became widespread at this time, its remains having being found at several Middle Miocene localities of the Greek-Iranian province, such as Paçalar and Prebreza, as well as in the Bugti beds of Pakistan. *Giraffokeryx* displayed two pairs of rather short, unbranched ossicones. The anterior pair was situated in front of the orbits, while the second pair arose directly behind the orbits. A second giraffid, *Georgiomeryx*, has also been found in some Middle Miocene localities of the Greek-Iranian province, like Chios in Greece and Byelometcheskaya in the northern Caucasus. *Georgiomeryx* was closely related to *Giraffokeryx* but displayed a unique pair of flat, laterally extended ossicones over the orbits and a more archaic dentition with brachydont teeth (de Bonis et al. 1997a).

In contrast with this highly diversified bovid and giraffid fauna, the cervoid representation in the open woodland areas of the Greek-Iranian province was extremely poor, almost reduced to primitive moschids of the genera *Hispanomeryx* and *Micromeryx*. Suids never attained the high diversity levels observed in western and central Europe, the ubiquitous *Listriodon splendens* becoming the most common element. The listriodontines evolved in a peculiar way in North Africa, leading to giant forms such as *Kubanochoerus*, which may have reached 800 kg in some cases. *Kubanochoerus* was found for the first time in the Caucasus (Byelometcheskaya) and probably derives from the African *Libyochoerus* (from the Early Miocene locality of Gebel Zelten). The most striking feature of these giant listriodontines was the presence in the males of an enormous horn above the orbits, which was probably used for intraspecific fighting and which indicates a unique case of territoriality in suids.

While the tetraconodonts, such as *Conohyus*, were dominant in western Europe, a group of archaic, small-sized suids, the sanitheres, persisted and succeeded in the Greek-Iranian province by developing selenodont cheek teeth. Their molarized premolars and molars bore wrinkled enamel formed of several cuspules and ridges, well adapted to browse on sclerophyllous vegetation (de Bonis et al. 1997b). A second browsing pig was *Schizochoerus*, a small peccary-like suid related to *Taucanamo* that developed lophodont molars and short, broad premolars.

This dentition resembles that of the contemporaneous advanced listriodontines and, as in that group, was probably well adapted to browsing in the vegetation of the sclerophyllous evergreen woodland, which covered most of the Greek-Iranian province at that time.

From the Asian side, members of the central Asian aceratherine hornless genus *Chilotherium* became the most common rhinos in the Greek-Iranian province. They were a group of grazing animals that occupied different niches and radiated into a number of (sub)genera such as *Subchilotherium* or *Acerorhinus*. Their legs were shorter than in any other aceratherine, mimicking those of the teleoceratines. A few of them were still clear browsers, like the brachydont *Acerorhinus*, while most of them were grass eaters (although certainly their diet included a number of nongraminean herbs). The shortening of the legs in this group can be explained by this grass-based diet. As aceratherines, they were hornless rhinos equipped with tusklike incisors probably used in fighting. Accordingly, but in contrast with the living grass-eater rhinos, the head maintained a horizontal position, so grazing was only possible after the shortening of the legs (Heissig 1989).

This time also records the first appearance of the hyenids (*Protictitherium*) in eastern Europe and western Asia. However, this does not mean in any way that the hyena-like scavenger niche was empty at that time, since a peculiar family of carnivores, the percrocutids, occupied that place in the Greek-Iranian province. The percrocutids seem to correspond to an early feloid radiation covering the "hyena guild," at a time when the true hyenids (*Protictitherium*) had not yet developed the dental and locomotory adaptations to scavenging and the bone-cracking characteristic of the later members of the family. The first percrocutids belong to the genus *Percrocuta* and are found in late Middle Miocene localities of western (Sansan, La Grive) and eastern Europe (Çandir, Paşalar), where they tended to coexist with the small, arboreal primitive hyenids of the genera *Protictitherium* and *Plioviverrops*. The Middle Miocene *Percrocuta* had not yet developed the bone-cracking adaptations which would be common in the Late Miocene members of the family (*Dinocrocuta*).

Southwestern Asia: The Environment of *Sivapithecus*

In contrast with the Greek-Iranian province, conditions were very different to the south of this region. Actually, the environment in southwestern Asia seems to have remained much closer to that in western and central Europe. According to the rich mammalian record of the Siwalik sequence in the Potwar Plateau (northern Pakistan), warm tropical-subtropical forest zones persisted in this area during most of the Miocene. Therefore, the Chinji and Nagri faunas, equivalent to those of the late Middle and early Late (Vallesian) Miocene of Europe, are basically composed of a mixed assemblage of archaic carnivores, poorly diversified browsing ruminants, and woodland/bushland omnivores (Bernor 1984; Barry et al. 1985). A number of large- to medium-sized browsers are reminiscent of the Greek-Iranian province, such as the sivatherine giraffids of the genus *Giraffokeryx* (*G. punjabiensis*), the rhino *Chilotherium intermedium*, or the small suid *Schizochoerus gandakasensis*. Despite these common elements, the faunas from the Kamlial and Chinji beds are very different from those of the Greek-Iranian province (including the Middle Miocene sites of eastern Africa such as Fort Ternan), maintaining low diversity levels of bovids and giraffids. Although the species are different, the Siwalik record includes taxa that are similar to those of the coeval western and central Europe faunas: proboscideans (*Deinotherium* sp.), rhinoceroses (*Brachypotherium permense*), chalicotherids (*Chalicotherium salinum*), suids (*Listriodon pentapotamidae*, *Conohyus sindiensis*, *Propotamochoerus hysudricus*, *Hippopotamodon* sp.), tragulids (several species of *Dorcatherium* and *Dorcabune*), carnivores (*Agnotherium* and other amphicyonids, nimravids like *Sansanosmilus* and *Barbourofelis*), cricetids (*Democricetodon* sp., *Megacricetodon* sp.), flying squirrels, and shrews. As in the case of western Europe, this assemblage strongly points to a rather closed, forested environment. Particularly significant is the presence of hominoids with climbing locomotory adaptations of the genus *Sivapithecus* (Pilbeam et al. 1996).

A case that is peculiar to the Siwaliks, and is not shared with western or eastern Europe, is the persistence of the anthracotherids, a family of archaic artiodactyls distantly related to the hippos. The anthracotheres were large suiforms with selenodont molars well adapted to a browsing regime. However, unlike the living suids, they still retained five digits on the forefeet and four on the hindfeet (although the lateral ones were more reduced). This was a unique combination of ruminant-like, selenodont dentition, coexisting with a generalist, pig or hippolike shape, with relatively short, stout legs and still functional lateral digits (actually, a combination very close to that of the living hippos). In the Middle to Late Miocene of Siwaliks, the anthracotherids are represented by two species of different size, *Microbunodon punjabiense* and *Hemimeryx* sp.

The observed differences between the sclerophyllous woodland faunas of the Greek-Iranian province and those from the Siwaliks can probably be explained on the basis of the lower latitudinal location of the latter region and the influence of the rising Tibetan Plateau on the development of the monsoonal climatic regime (Kutzbach et al. 1993). The Potwar Plateau is flanked to the north and the west by north-south lying Sulaiman and Kirthar ranges and Baluchistan and Sind. The uplift of these encircling mountain ranges would have trapped moist Indo-Pacific monsoons of the slopes facing the Siwaliks and nourished the less seasonal environments there (Bernor 1984).

The Hipparion Dispersal Event

Between 12 and 11 Ma, a drastic cold pulse led to a new growth of the Antarctic Ice Sheet and a global sea-level fall of about 140 m (Haq et al. 1987). The oceans dropped about 90 m below the present sea level, and a number of land bridges came again into existence, thus enabling faunal exchange between previously isolated terrestrial domains. As a consequence, a new corridor was reestablished between

Asia and North America across what is now the Bering isthmus. The main result of the reopening of this land bridge was the quick dispersal into Eurasia of the hipparionine horses of the genus *Hipparion* and their relatives.

The hipparionine horses arose in North America during the Middle Miocene and differed significantly from *Anchitherium* and other similar equids in the development of very high-crowned cheek teeth as a response to the more sclerophyllous, harder vegetation. Moreover, the tooth enamel became folded in several ridges, which were in their turn filled with dental cementum. The two persisting lateral toes in the hipparionine horses became more reduced than in *Anchitherium*, thus concentrating most of the body weight on the central toe. After the establishment of the Bering land bridge, the hipparionine horses quickly invaded the whole of Eurasia, from China to Iberia, their presence having been reported from hundreds of fossiliferous localities. Existing data suggest that, after their entry into Eurasia, the hipparionine horses spread very quickly across Europe, their presence having been reported at 11.1 Ma both in the Vienna and the Vallès-Penedès Basins (Garcés et al. 1997). They probably colonized first the more northern latitudes of Asia and spread later to the south and east. The dispersal of the hipparionine horses appears therefore as an Old World event and defines the lower boundary of the Vallesian Mammal Stage, the continental equivalent of the early Late Miocene in Eurasia. *Hipparion primigenium*, the first hipparionine species to enter Europe, was a relatively large form standing about 1.5 m at the withers (the stature of a Burchell's zebra). Its slender axial skeleton suggests it was well adapted for leaping and springing rather than for sustained running and high speed (Bernor and Armour-Chelu 1999). This and other archaic hipparionine horses are included by some authors in the separate genus *Hippotherium.*

Although a single taxon event, the dispersal of *Hipparion* dragged on other immigrants from the open woodlands of central and western Asia into the laurophyllous forests of western Europe. This was the case for the first European leporids of the genus *Alilepus*, the sivatherine giraffids of the genus *Decennatherium*, and the saber-toothed felids of the genus *Machairodus*. Among lagomorphs, the leporids (the family that includes the living hares and rabbits) had a long evolutionary history in North America since the Eocene. However, it was not until the Early Vallesian that they settled in Europe, at that time still dominated by the pikas of the genus *Prolagus*. Another immigrant in this time, *Decennatherium*, was one of the first members of the sivatherines, a lineage of large, robust giraffids which differed from the more slender *Palaeotragus* in the possession of not two but four ossicones, a first pair over the orbits and a second larger pair at the rear of the skull. The sivatherines became the dominant giraffids of the Late Miocene terrestrial ecosystems and persisted in Africa until the Early Pleistocene, coexisting with the first hominids. As in the case of other primitive sivatherines, such as *Bramatherium* and *Hidaspitherium*, from the Siwalik Hills in Pakistan, *Decennatherium* probably had an enlarged anterior pair of ossicones (or a unique fused anterior ossicone) and a less prominent posterior pair. Its limb bones were longer and more slender than the later members of this group.

Another typical Early Vallesian newcomer was *Machairodus*, a large saber-toothed cat that coexisted with the last nimravids of the genus *Sansanosmilus*. Apart from the large amphicyonids, all the other Middle Miocene hypercarnivorous predators were relatively small forms of less than 100 kg, but members of the genus *Machairodus* were large saber-toothed cats which could attain 220 kg (the size of a lion). As in the case of nimravids, the most characteristic feature of these predators was their long, laterally compressed and flattened upper canines, which greatly surpassed the size of the lower ones. The first machairodontine cats are recorded in the Middle Miocene of the Greek-Iranian province and persisted there until the Early Vallesian (*Miomachairodus pseudailuroides* from Yeni-Eskihisar and Eşme-Akçaköy in Turkey). *Machairodus aphanistus* is the most common Late Miocene species in Eurasia, ranging from the Iberian Peninsula to North America. Its limb anatomy was very different from that of the modern cats, with forelimbs longer and more robust than the posterior limbs, a feature which enabled them to grasp and immobilize their prey (Turner and Antón 1997). It seems that, at a first glance, the entry of *Machairodus*, a felid filling the large predator guild previously occupied by *Sansanosmilus*, would have had serious consequences for these nimravids, including their final extinction by competition. However, this was not the case and both *Machairodus* and *Sansanosmilus* coexisted for more than a million years without replacement of one by the other. A similar case was found in the Greek-Iranian province, where the large nimravid *Barbourofelis* coexisted with *Miomachairodus* in the Early Vallesian beds of the Sinap Formation in Turkey. *Barbourofelis* was larger than *Sansanosmilus*, the size of a lion, and in the Late Miocene attained a very broad distribution, from North America to eastern Europe.

The diversity also increased among the large browser perissodactyls such as rhinos and tapirs. From the rhino side, the most common form at that time was *Aceratherium*. This hornless aceratherine, close to the Middle Miocene *Hoploaceratherium*, was one of the most long-lasting genera of the Late Miocene, surviving until the Miocene-Pliocene boundary about 5 Ma. It was a medium-sized rhino with long limbs and a still functional fifth metacarpal. The cheek teeth were brachydont, indicating a browsing diet based on leaves and soft vegetation. Its limb proportions, close to those of the living tapirs, suggest a similar lifestyle (Heissig 1989). The males of *Aceratherium incisivum* bore a pair of strong tusks which enabled them to browse the dense vegetation of the Early Vallesian laurophyllous woodlands. As in other aceratherines, these tusks were much smaller in the females. In the Greek-Iranian province, other advanced rhinos of probable African origin joined *Chilotherium* in the Late Miocene. This was the case of *Ceratotherium*, the genus that includes the living white rhino. The early representatives of *Ceratotherium* (*C. neumayri*) were only partly grass eaters, but a trend is observed in this group throughout the Miocene and the Pliocene to develop more open-country adaptations such as large body dimensions and slightly hypsodont cheek teeth.

Another group of perissodactyls that flourished at this time were the tapirs (*Tapirus priscus*), which reappeared in western Europe after their disappearance in the very Early Miocene. The anchitherine horses were represented by larger, more advanced species of *Anchitherium* which developed longer limbs and higher-crowned dentitions. These anchitherine horses persisted in central Europe until the latest Vallesian, although in some regions (Spain) they disappeared shortly after the entry of the first hipparionine horses. Among the smaller browsers, peculiar elements in Europe were the hyraxes, which are found at a number of Vallesian localities such as Can Llobateres (Vallès-Penedès, Spain), Melambes (Crete, Greece), and Eşme-Akçaköy (Turkey). Despite its small size and rabbitlike appearance, the hyraxes are archaic ungulates that today inhabit the rocky and steppe environments of central and southern Africa (although its range extends up to Lebanon). Their molars are brachydont and selenolophodont, strongly resembling those of some archaic perissodactyls. Although the living hyraxes are hare sized (about 50 cm in length), the Late Miocene European forms such as *Pliohyrax* reached large body dimensions, comparable to those of a tapir. The first hyraxes that settled in Europe in the Early Vallesian certainly had an African origin. Therefore, a limited exchange with northern Africa still existed in the Early Vallesian, although the possibility that hyraxes entered with the dryopithecids at the end of the Middle Miocene cannot be excluded.

Among the carnivores, the large amphicyonids of the species *Amphicyon major* persisted. The hypercarnivorous and cursorial amphicyonids *Thaumastocyon dirus* and *Agnotherium antiquus* persisted also in the Early Vallesian. *Agnotherium antiquus* is a poorly known species present in several localities from western and central Europe (Pedregueras, Eppelsheim, Rudabanya) and known also from northern Africa (Bled Douarah). It was similar to the better known Middle Miocene *Agnotherium grivensis* but smaller in size (160 kg). Among the bears, the small omnivorous ursids of the genus *Ursavus* diversified into the species *U. brevirhinus* and *U. primaevus*, while the mesocarnivore *Hemicyon* was represented by *H. goeriachensis* (of about 120 kg). But the most significant event in this group was the appearance of the first large ursids of the genus *Indarctos*. *Indarctos vireti*, of about 175 kg, was the first member of a lineage of large mesocarnivore ursids, which were characteristic elements of the Late Miocene carnivore community.

In the Early Vallesian, the true hyenids were still represented by the civetlike *Protictitherium*, the mongoose-like *Plioviverrops*, and the wolflike *Thalassictis*. At this time, *Protictitherium* also colonized northern Africa, being present in the Early Vallesian of Tunisia (*P. punicum*). The cursorial canidlike hyenid guild was enriched with new forms close to *Thalassictis* such as *Ictitherium* and *Hyaenictitherium*. Both may have been originated in the Greek-Iranian province or elsewhere in Asia and spread later into Europe. This time also records a high diversity of old viverrids (such as *Semigenetta ripolli* from Can Llobateres) and mustelids, which inherited the variety of forms present at the Middle Miocene: badgers (*Sabadellictis*), skunks (*Promephitis*, *Mesomephitis*), otters (*Sivaonyx*, *Limnonyx*, *Lutra*), wolverines, and glutton-related forms (*Trochictis*, *Circamustela*, *Marcetia*, *Plesiogulo*). Some of these glutton-related forms were relatively large sized for a mustelid, reaching 50 kg in the case of *Hadrictis* and *Eomellivora*.

Therefore, despite its significant zoogeographic importance, the spread of the hipparionine horses and their cohort of Asian immigrants was a quite limited event which did not result in a significant change in the structure of the previously existing western Old World mammalian communities. Newcomers like *Machairodus*, *Alilepus*, *Hipparion*, or *Decennatherium* joined the already highly diversified western European faunas without a clear and immediate replacement of the potential competitors which were there occupying similar guilds. The same situation is observed in the Potwar Plateau, where no significant mammal turnover is associated with the entry of *Hipparion*. Only the extinction of older species, notably suids and cricetids, is recorded at the base of chron C5N (ca. 10.8–10.9 Ma), shortly before the first occurrence of this equid in the Siwaliks sequence (Barry et al. 1985; Pilbeam et al. 1996). The Early Vallesian faunas in Europe are thus characterized by the "peaceful" coexistence of a number of species which seem to have filled similar ecological guilds. This led to a sort of "climax" situation in the western European ecosystems, which reached levels of mammalian diversity unknown in any other Late Cenozoic epoch. With more than 60 mammal species, localities such as Can Ponsic and Can Llobateres 1 in Spain or Rudabanya in Hungary are good examples of these Early Vallesian "inflated" faunas. Despite the presence of new immigrants like *Hipparion*, *Decennatherium*, or *Machairodus*, the western European Vallesian ecosystems were composed of almost the same elements that populated the Middle Miocene subtropical forests, retaining a similar community structure. In this environmental context, the Eurasian hominoids reached an extraordinary diversity, which included the forest-adapted, suspensor *Dryopithecus* and *Sivapithecus*; the dry-adapted *Ankarapithecus*; and the robust, gorilla-like *Graecopithecus*.

The Vallesian Crisis

After the high diversity levels attained in the Early Vallesian, an abrupt decline in the Vallesian mammalian faunas took place at about 9.6 Ma in what is known as the Vallesian Crisis (Agustí and Moyà- Solà 1990; Agustí et al. 2013). The Vallesian Crisis was first recognized in the Vallès-Penedès Basin of Spain and involved the sudden disappearance of most of the humid elements that characterized the Middle Miocene and Early Vallesian faunas from western Europe. Among the large mammals, this crisis particularly affected several groups of perissodactyls such as the rhinoceroses *Lartetotherium sansaniense* and "*Dicerorhinus*" *steinheimensis* and the tapirs (only the small tapirs of the badly known *Tapiriscus pannonicus* persisted until the Early Turolian in central Europe; Franzen and Storch 1999). These losses were only partly compensated by the entry just before the onset of the Vallesian Crisis of *Dihoplus schleiermacheri*, a large species of browsing rhino which bore a pair of massive horns and was the largest rhino of its time. Among the artiodactyls, the high diversity attained by the suids in the Early Vallesian times suddenly dropped and several characteristic elements vanished. This was the case for the browsers *Listriodon* and *Schizochoerus* (which made a short-lived incursion in western Europe at the beginning of the Late Vallesian), as well as for the tetraconodontines *Conohyus* and *Parachleuastochoerus*. In contrast, the "modern" suinae, such as *Propotamochoerus*, persisted and even enlarged their diversity with a new eastern immigrant *Microstonyx*. *Microstonyx* was a giant pig (about 300 kg), with a skull more than half a meter long. The Vallesian Crisis also involved the final decline of the Middle Miocene forest community of cervoids (the cervid *Amphiprox* and the moschid *Hispanomeryx*) and the spread of the boselaphine bovids like *Tragoportax*, which replaced their semiaquatic relatives of the genus *Protragocerus*. *Tragoportax* was a medium-sized bovid of about 80 kg with relatively long limbs, which suggests that it was a fast runner and a good jumper which lived in the open woodland. It possessed a short-faced skull with a long neurocranium and large backwardly curved horns. The teeth were high crowned and with cementum, resembling those of the living *Boselaphus* (Köhler 1993).

Among the rodents, the Vallesian Crisis involved the disappearance of most of the cricetids and glirids of Early or Middle Miocene origin (*Megacricetodon*, *Eumyarion*, *Bransatoglis*, *Myoglis*, *Paraglirulus*, *Eomuscardinus*), flying squirrels (*Albanensia*, *Miopetaurista*), and beavers (*Chalicomys*, *Euroxenomys*). However, other less diversified small mammal groups, such as lagomorphs and insectivores, remained almost unaffected by this crisis. In western and central Europe, this event coincided with the first dispersal of the murid rodents, the family that includes the living mice and rats. After their entry into Europe, this group became the dominant rodents in the Late Miocene communities and diversified into a number of genera: *Progonomys*, *Occitanomys*, *Huerzelerimys*, and *Parapodemus*.

Another group which was severely affected by the Vallesian Crisis was the large carnivores of the families Nimravidae and Amphicyonidae. Among the amphicyonids, all the genera and species still existing in the Early Vallesian disappeared: *Pseudarctos bavaricus*, *Amphicyon major*, and *Thaumastocyon dirus*. Only some poorly known *Amphicyon* representatives persisted in the Late Vallesian and Early Turolian in some parts of central Europe. Among the ursids, the Vallesian Crisis had an ambivalent effect. While the slender cursorial forms of Early Miocene origin like *Hemicyon* vanished, the robust ursids of “modern” aspect persisted, represented by larger species. This was the case with *Indarctos*, represented by the species *I. vireti* and *I. arctoides*, as well as *Ursavus* represented by *U. depereti*, the largest species of the genus. In turn, the mustelids were severely affected by the Vallesian Crisis, which involved a significant decrease in the once highly diversified Vallesian fauna.

At the same time, a number of eastern immigrants appeared for the first time such as the large hyenids of the genus *Adcrocuta* and *Hyaenictis*. These genera represent two opposite trends in the evolution of Late Miocene hyenids. *Hyaenictis* was a cursorial meat and bone eater, which prolonged the trend initiated by *Thalassictis* toward increasing cursoriality. They show also a trend toward the reduction of the bone-crushing portion of their dentition, developing and extending at the same time the sectorial part, so that the posterior molars were reduced or lost. At the other end of the scale, *Adcrocuta*, at about 70 kg, was the first representative of the modern bone-cracker hyenids leading to the living *Crocuta* and *Parahyaena*. They were characterized by advanced adaptation to bone crushing, with enlarged bone-cracking premolars. *Adcrocuta* had short stocky limbs, indicating that it was not a cursorial form. Like *Hyaenictis*, it was of probable Asian origin.

Among the large predator guild, the nimravids finally came to an end with the Vallesian Crisis, after representing the "large cat" guild for millions of years. Their extinction was compensated with the entry of *Promegantereon*, a new genus of machairodontine cats. *Promegantereon ogygia*, the oldest species of this genus, was smaller and more slender than *Machairodus aphanistus* (about 44 kg), retaining the archaic anatomy inherited from its ancestor *Pseudaelurus quadridentatus*. With their robust forelimbs and slender hind limbs, the members of this species were probably able to climb trees, carrying large prey as do living leopards. Their long muzzled skull was also superficially leopard-like, although, as a true machairodont, their upper canines were characteristically long and laterally flattened (Turner and Antón 1997).

Last but not least, the Vallesian Crisis led to an abrupt end of the hominoid experiment in Europe. Hominoids like *Dryopithecus*, *Ankarapithecus*, or *Graecopithecus* disappeared entirely from the fossil record, and only *Oreopithecus* in its island refuge and *Sivapithecus* in southwestern Asia survived this extinction event (see the next sections). *Dryopithecus* is still found in some early Late Vallesian localities dated at about 9.6 Ma (Can Llobateres 2, Viladecavalls) but disappeared from the fossil record shortly after. In the Greek-Iranian province, the robust *Graecopithecus* also disappeared at the beginning of the Late Vallesian. A similar case was that of the Turkish *Ankarapithecus*, its record ending again in the Late Vallesian. The extinction of these robust hominoids in this province coincides with the spread of the colobine monkeys of the genus *Mesopithecus*. This was not the case in western Europe, where the extinction of the slender dryopithecines did not involve its replacement by any other kind of primate species. Only the persistence until the latest Vallesian of the advanced folivorous pliopithecids of the genus *Anapithecus* can be quoted in this area, some hundred thousand years after the last *Dryopithecus*. In China, the pliopithecids survived even longer, until the latest Miocene, being represented by a large-sized form (*Laccopithecus*).

Causes of the Vallesian Crisis

What could have caused the set of extinctions and deep faunal restructuring which took place at 9.6 Ma during the Vallesian Crisis? Some evidence, such as the exit of several forest forms and the development of sigmodont teeth by some groups of rodents, would support the replacement at that time of the laurophyllous forests by grasslands. However, the spread of grasses over large extensions of Eurasia has been dated by Cerling and coworkers to between 8.3 and 7 Ma, and geochemical analyses carried out on teeth and soil nodules older than that timespan do not detect any sign of such an environmental change. Nevertheless, the fact that this major ecological restructuring of the western European mammal assemblages affected especially those taxa with tropical forest affinities, and the latitudinal character of these extinctions (a number of forest-adapted taxa survived until the Early Turolian in central Europe), strongly suggests its climatic forcing. This is supported by the Late Miocene oceanic evolution, which was a continuation of the processes started at the Middle-Late Miocene transition. Enhancement of the latitudinal thermal gradient resulted in the generation of new erosive oceanic surfaces (NH5) by intensification of the deep circulation. Further cooling resulted in new δ^{18}O-positive shifts (i.e., Mi6 and Mi7; Miller et al. 1987, 1991). Changes in benthic and planktonic assemblages also indicate colder climatic conditions and increasing isolation between low and middle latitudes. All these oceanic changes were nearly synchronous with some significant changes in low-latitude Old World terrestrial domains. In particular, there is a noticeable synchronism between the Mi7 isotopic shift at 9.3–9.6 Ma and the age of 9.6 Ma obtained for the Vallesian Crisis in the Vallès-Penedès stratigraphic sections. The Vallesian Crisis is also close to the beginning of the NH5 hiatus, one of the most important sets of deep oceanic discontinuities recognized in the Late Miocene (Keller and Barron 1983), which is dated between 9.0 and 9.5 Ma. NH5 has been also related to a period of cooling and major restructuring of the deep oceanic circulation and to the growth of ice sheets in western Antarctica (Keller and Barron 1983).

But how did these changes affect the composition of the terrestrial vegetation? A change to more open environments did not start until 8 Ma, the extension of grasslands taking place almost 2 Myr after the Vallesian Crisis. The pre-Vallesian floras in the region indicated the persistence of humid subtropical conditions, with abundance of broad-leaved mega-mesotherm elements such as *Ailanthus*, *Caesalpinia*, *Cassia*, *Cinnamomum*, *Ficus*, *Sapindus*, etc. (Sanz de Siria 1994). Indeed, the very rich mammal locality of Can Llobateres 1 yielded remains of some of these subtropical elements such as *Sabal*, *Ficus*, and others. However, we know that the laurophyllous subtropical woodland prevailing until the beginning of the Late Miocene in Europe was profoundly affected in some way. The answer arrived in 1994, when for the first time a well-calibrated Late Vallesian flora was discovered in a section close to the city of Terrassa in the Vallès-Penedès Basin (Sanz de Siria 1997). This flora has been dated by paleomagnetism at somewhat more than 9 Ma and therefore records the kind of vegetation that was dominant just after the Vallesian Crisis (Agustí et al. 2003).

The flora from the Terrassa section includes 36 different taxa from the families Lauraceae, Ulmaceae, Hamamelidaceae, Juglandaceae, Myricaceae, Fagaceae, Betulaceae, Tiliaceae, Salicaceae, Ericaceae, Sapotaceae, Myrsinaceae, Celastraceae, Aquifoliaceae, Rhamnaceae, Sapindaceae, Aceraceae, Oleaceae, Poaceae, and Typhaceae. Close to 45 % of this flora is composed of deciduous trees such as *Acer*, *Alnus*, *Fraxinus*, *Carya*, *Juglans*, *Populus*, *Parrotia*, *Zelkova*, *Ulmus*, or *Tilia*, that is, the elements that are now dominant in the temperate forests of the middle latitudes. In contrast, warm evergreen elements, represented by *Myrsine*, *Sapindus*, *Sapotacites*, etc., decreased to 7 %. Supporting the argument that this change was not related to the extension of grasslands was the persistence of a "hard core" of subtropical elements, represented by 33 % of evergreen trees, able to endure a certain level of seasonality, and which persisted in Europe until the Early Pliocene (*Laurophyllum*, *Laurus*, *Rhamnus*, *Daphnogene*, and others). The existence at that time of a dry season (summer drought) is confirmed by the presence at Terrassa of a 15 % of Mediterranean or pre-Mediterranean taxa

(*Quercus* cf. *ilex*, *Q. praecursor*). From a physiognomic point of view, 56.4 % of the species display leaves with entire margins, while the remainder present dentate or serrated margins. Regarding leaf size, most of the taxa are microphyllous (83.3 %) or nanophyllous (10 %).

According to these data, the Terrassa association is comparable to floras that are found today in parts of central-east China, south Japan, eastern North America, and North Africa, where a similar mixture of evergreen broad-leaved, warm-temperature, and deciduous elements is present (Wang 1961; Barbero et al. 1982; Richardson 1990; Barbour and Chistensen 1993). In these regions, similar mega-mesotherm taxa (*Lauraceae*, *Myrsine*, *Sapotacites*, *Sapindus*, and others) are concentrated in the lower levels of vegetation, with mean annual temperatures between 16 °C and 19 °C and mean annual precipitation levels above 1,000 mm. A clear winter season is already present at this stage. In some areas, drier, sclerophyllous elements (*Q. ilex*, *Rhamnus*, *Rhus*) coexist with the former ones. An evergreen broad-leaved forest is present at a medium stage because of the concentration of humidity due to the marine influence (*Cinnamomum*, *Persea*, *Laurus*, etc.). At higher altitudes a deciduous broad-leaved forest (including most of the temperate, deciduous elements like *Acer*, *Fraxinus*, *Juglans*, *Populus*, *Quercus*, *Tilia*, *Zelkova*, and others) is dominant. Mean annual temperatures at this stage decreased to around 12 °C. Therefore, a similar zonation probably developed in the transition from the Early to the Late Vallesian, causing a significant decrease of Middle Miocene evergreen elements (33 %) and the expansion of a deciduous broad-leaved forest at a medium stage (45 % of deciduous elements), where intake of fruit during the winter season must have been much more difficult.

The flora from Terrassa suggests that the deep faunal change at 9.6 Ma was not the consequence of the replacement of the subtropical Miocene forest by grasslands but rather the substitution of one kind of woodland by another. The intensification of the thermal gradients between the middle and low latitudes, probably enhanced by the Himalayan and Tibetan uplifts, led to an abrupt change in the previously existing evergreen subtropical woodlands of western Europe. These were probably replaced by an association in which more seasonally adapted, deciduous trees were dominant. Rather than the moderate cooling associated with the Mi7 isotopic shift, it was this change in the structure of the vegetation which determined the set of extinctions that took place during the Vallesian Crisis.

Most members of this fauna, including *Dryopithecus* and other European hominoids, were mainly frugivorous, with a diet based on fruits and the soft vegetables common in the evergreen broad-leaved forests of the Early and Middle Miocene. Therefore, although the decrease in temperature and increasing latitudinal gradient had little direct effect on the Vallesian mammals, the replacement of most of the evergreen trees by deciduous ones, well adapted to the new conditions of seasonality with colder winters and dryer summers, had much more dramatic effects. In this way, a number of elements, such as certain pigs, rodents, and primates, had to subsist during several months without fruit, a basic and highly nutritional component of their diet. This dietary factor, and not the extension of grasslands or the shift of temperature, was probably the direct agent that caused the abrupt drop of the rich Early Vallesian faunas.

In turn, the sudden disappearance of most of the medium-sized herbivores that had lived in Europe for millions of years probably led to a critical situation for the old predators of Middle Miocene origin, such as the nimravids and the amphicyonids, which until the Early Vallesian had successfully endured the competition from the machairodont cats and the large ursids. These carnivores were also indirect victims of the vegetation change that took place 9.6 Ma. An interesting element is that, contrary to *Dryopithecus*, the crouzeline pliopithecid *Egarapithecus* survived the Vallesian Crisis, a fact that is probably related to a folivorous rather than frugivorous diet.

Asian Survivors

The general absence of long sections of Vallesian age makes difficult the recognition of the Vallesian Crisis in other Old World regions, although there exist significant exceptions. In the well-calibrated succession of the Potwar Plateau in central Asia, a significant decay in the relative abundance of tragulids (from 45 % to 10 % of ruminant artiodactyls; Barry et al. 1991) is observed between 9.8 and 9.3 Ma, while the bovids became the dominant artiodactyls in the area (from 45 % to 80 %; Barry et al. 1991). However, the changes operating at 9.6 Ma in the region of the Siwaliks can hardly be compared with the dramatic effects of the Vallesian Crisis in western Europe. In contrast with Europe, the mammal faunal association linked to the existence of warm tropical-subtropical forested zones persisted in Siwaliks until chron 4r, at 8.3 Ma. It still included archaic carnivores and rhinoceroses (*Brachypotherium*), proboscideans (*Deinotherium*), dormice, shrews, and hominoids with climbing adaptations (*Sivapithecus*). As we have seen, the persistence of this kind of fauna in the Late Miocene of the Siwaliks can probably be explained by the settling of monsoon atmospheric dynamics in the latter region, which could have maintained the forested subtropical conditions there until 8.3 Ma.

However, between 8.3 and 7.8 Ma, a set of extinctions similar to those of the earlier Vallesian Crisis took place (Pilbeam et al. 1996). Several cricetid, bovid, and tragulid species disappeared, and the hominoid *Sivapithecus* was replaced by colobine monkeys. These faunal changes coincide in the southwestern central Asian region with a shift in the $\delta^{13}C$ isotopic composition of the paleosoil and dental carbonates, indicating a climatically forced change from a forest and woodland vegetation in which C_3 plants (trees and bushes) were dominant to grasslands dominated by grasses and other C_4 plants (Quade et al. 1989; Morgan et al. 1994; Cerling et al. 1997). They were also largely coeval to further oceanic cooling (White et al. 1997), development of extensive oceanic erosive surfaces (NH6) and development of ice sheets in the Arctic (Eyles 1996). Therefore, the change from C_3- to C_4-dominant vegetation had dramatic effects to the south of the Himalayas and led to the development of an open woodland also in southwestern Asia.

However, *Dryopithecus* may have subsisted for more time in some refuges of western Eurasia. One of these refuges seems to have been the southern Caucasus, where the presence of a slender dryopithecine (*Udabnopithecus garedziensis*, actually a small form of *Dryopithecus*) was reported a long time ago in the Early Turolian beds of Udabno (Georgia; Gabunia et al. 2001). According to its mammalian association, the age of the Udabno levels is close to 8.5 Ma. It means that *Dryopithecus* or another genus of thin-enameled hominoids persisted in the Black Sea region when this kind of primates went extinct elsewhere in Europe. The persistence of the evergreen subtropical forests to the south of the Caucasus, linked to the retention of special climatic conditions, probably enabled *Udabnopithecus* to survive in this region.

In Asia, the dryopithecines may have survived for longer in the Late Miocene, as suggested by the presence of *Lufengpithecus* in the Late Miocene of Chiang Muang, in Thailand (Chaimanee et al. 2003; Pickford et al. 2004), and Keiyuan and Lufeng in China (Zhang Xingyong 1987; Harrison et al. 2002). Chiang Muang presents a typical pre-*Hipparion* fauna with gomphotherids (*Tetralophodon* cf. *xiaolongtanensis*), rhinos (*Chirotherium intermedium*), peccaries (*Pecarichoerus sminthos*), large suids (*Hippopotamodon* cf. *hyotherioides*), tetraconodontine suids (*Conohyus sindiensis*, *Parachleuastochoerus sinensis*), and tragulids (*Dorcatherium* sp.) in a wooded context that resembles that of the late Middle Miocene of western Europe and Siwaliks. Similar in age and environment is the locality of Keiyuan, in China, which presents the same kind of hominoid (*Lufengpithecus keiyuanensis*). *Lufengpithecus* is still present in type locality of the genus, Lufeng, a site dated in 8 Ma (equivalent, therefore, to the Early Turolian levels of Europe).

The *Oreopithecus* Fauna: Survivors in an Island Environment

Even more significant was the case of *Oreopithecus*, an enigmatic hominoid which lived in the Tuscany area (northern Italy) from 9 to 7 Ma. At the time when *Oreopithecus* occupied the Tuscany region, Italy had a very different aspect from today. The territories which form the present Italian peninsula were in the Early Turolian an arch of isolated islands which extended from central Europe to northern Africa. One of these islands, close to the European mainland, was formed by Tuscany and the Corso-Sardinian block. A number of European immigrants settled in this area at some time between the Vallesian and the Turolian and persisted there until the end of the Miocene. The *Oreopithecus* faunas appear in several localities from Tuscany, like Casteani, Montebamboli, Ribolla, Montemassi, and also Fiume Santo in Sardinia. However, the best sequence is recorded in the Bacinello Basin, again in Tuscany, where a succession of fossiliferous levels has been recorded (Rook et al. 1999).

The lowermost ones, called V 0 and V 1, are Early Turolian in age and still include some “common,” nonendemic elements like the cricetid *Kowalskia* and the murids *Huerzelerimys* and *Parapodemus*. However, most of the *Oreopithecus* faunas of the Baccinello levels V 1 and V 2 are basically composed of endemic elements.

These faunas appear as a sort of impoverished, "miniaturized" Vallesian ecosystem. Thus, although already modified by the new insular conditions, most of the large mammalian components of this Late Miocene immigration wave can be referred to common elements of the Late Vallesian or Early Turolian European ecosystems, such as hypsodont bovids (*Thyrrenotragus*, *Maremmia*), giraffids (*Umbrotherium*), *Microstonyx*-like suinae (*Eumaiochoerus*), dryopithecids (*Oreopithecus*), or *Indarctos*-like ursids. *Umbrotherium* is a poorly known giraffid, probably related to a sivatherine stock. *Thyrrenotragus* and *Maremmia* were small bovids with very hypsodont dentitions. Both forms were once interpreted as African immigrants in the area: *Tyrrhenotragus* as a neotragine (the tribe that includes dwarf antelopes and gazelles) and *Maremmia* as a precocious alcelaphine (the tribe that includes the African gnus, hartebeests, and impalas). However, some of the features that relate them to these African groups, like the short metapodials of *Thyrrenotragus* and the probably ever-growing incisors of *Maremmia*, could have developed independently as specializations linked to an island environment. A small suid, *Eumaiochoerus*, is also present in the lignites of Bacinello (V 2) and in Montebamboli. It bore a short snout, elongated spatulate upper incisors and small-sized, chisel-shaped lower tusks. Despite these dental specializations and its small size, other features closely relate this endemic suid to the large *Microstonyx major*.

However, other elements in the Baccinello succession suggest that a previous Middle Miocene faunal background already existed on the Tusco-Sardinian Island before the Late Miocene settlement of *Oreopithecus* and its allies. This is the case, for instance, of *Anthracoglis*, a dormouse close to the Middle Miocene *Microdyromys* and *Bransatoglis* but significantly larger. A second unnamed giant dormouse is scarcely present in the level V 1 of Baccinello. Besides these endemic dormice, a third small mammal, the lagomorph *Paludotona*, is present in the V 1 level. *Paludotona* was an ochotonid whose body dimensions were again larger than those of its coeval relatives in Europe. The most striking feature of *Paludotona* is its archaic dental morphology, which relates it to some Early to Middle Miocene ochotonids like *Lagopsis*. But the last *Lagopsis* disappeared from Europe in the Middle Miocene, some million years before the deposition of the Bacinello lignites! It seems therefore that at the time of deposition of the V 1 level, there was a long history of isolation on the Tusco-Sardinian Island. The existence of a previous Early to Middle Miocene settlement of the Tusco-Sardinian Archipelago is also supported by the presence in Casteani (equivalent to level V 1 of Bacinello) of an anthracothere. The Tuscan anthracothere is a very archaic one which clearly differs from the advanced Late Miocene anthracotherids of northern Africa. Since the last anthracotheres disappeared from Europe in the Early Miocene, its presence in this area can only be explained as a result of an immigration event from Africa or by assuming its persistence as an Early Miocene relict as in the case of *Anthracoglis* and *Paludotona*.

The environment in which the *Oreopithecus* fauna developed was a mixed mesophytic forest, similar to those that today are found in east central China along the Yangtze River. Thus, tropical-subtropical trees, like *Engelhardia*, and warm-temperate trees and shrubs, like *Taxodium*, *Myrica*, etc., are well represented in the pollen analysis of the levels V 0 and V 1 of Bacinello, while more temperate and Mediterranean elements, such as *Quercus*, *Carpinus*, *Tilia*, *Carya*, *Pterocarya*, etc., are rare (Harrison and Harrison 1989; Benvenuti et al. 1994). The pollen analysis developed in the level V 2 shows an increase in temperate, cold-temperate, and mountain elements such as *Picea* and *Abies* (Benvenuti et al. 1994). However, a cold phase cannot clearly be recognized due to the scarcity of grains of elements such as *Tsuga* or *Cedrus*. The increase of temperate and cold-temperate trees in the level V 2 of Baccinello may be the result of a change in the climatic conditions (as in the case of the Late Vallesian floras) but could also be associated with the uplift of the Tuscan area.

The Tusco-Sardinian experiment came finally to an abrupt end when a connection to the continent was established at about 6.5 Ma. New herds of European immigrants entered the Tusco-Sardinian area, including such large predators as *Machairodus* and *Metailurus*. Not surprisingly, *Oreopithecus* and the other endemic elements of the Tuscan fauna underwent a rapid extinction, unable to resist the competition of the continental newcomers. This change in the faunal composition is also paralleled by a vegetation change. Therefore, the pollen analysis developed in the V 3 unit of Bacinello shows an increase in herbs (Chenopodiaceae, Compositae, Dipsacaceae, etc.) and sclerophyllous trees (*Pinus* t. *haploxylon*, *Cathaya*; Benvenuti et al. 1994). The *Oreopithecus* experiment came to an end, and the Tusco-Sardinian biome finally followed the general trend toward more open and dry environments that was dominant in the whole of Eurasia.

The Late Miocene African Record

As in other parts of the Old World, the beginning of the Late Miocene in Africa is characterized by the dispersal of the first hipparionine horses on this continent. As happened in Europe, the entry of these hipparionine horses at the beginning of the Sugutan (an African equivalent of the Eurasian Vallesian) did not involve a significant restructuring of the existing terrestrial ecosystems. Most of the elements which composed these ecosystems at the beginning of the Late Miocene in Africa were close relatives of similar taxa in western Eurasia. Faunas of this age, such as those of the Ngorora Formation (Tugen Hills, Kenya; Hill et al. 1985), Narumungule Formation (Samburu Hills, Kenya; Nakaya 1994), or Chorora Formation (Ethiopia; Geraads et al. 2002), are based on a mixture of Middle Miocene African survivors associated with several elements that are common to the Siwaliks and Greek-Iranian provinces. Large browsers include proboscideans (*Choerolophodon*, *Tetralophodon*, *Deinotherium* cf. *bozasi*), rhinos (*Chilotheridium*, *Paradiceros*, *Brachypotherium*), chalicotheres (*Ancylotherium*), hipparionine horses (*Hippotherium primigenium*), and a variety of ruminants of western Eurasian affinities (*Palaeotragus*, *Samotherium*, *Protagocerus*, *Miotragocerus*, *Palaeoreas*/*Sivoreas*, *Homiodorcas*, *Ouzoceros*, *Pseudotragus*, *Pachytragus*, *Gazella*). The persistence of forest conditions is indicated by the presence of tragulids (*Dorcatherium pigotti*) and gliding rodents (*Paranomalurus*). However, the presence of an iranotherine rhino (*Kenyatherium*) at Narumungule suggests the existence of more open conditions close to the woodlands. Typical African components of these faunas are the climacoceratid giraffoids (*Climacoceras*), listriodontine, and tetraconodontine suids (*Lopholistriodon* and *Nyanzachoerus*), and archaic hippos (*Kenyapotamus coryndoni*). As happened at the beginning of the Vallesian in Europe, the dispersal of the hipparionine horses involved other Asian elements, such as the saber-toothed machairodontine cats and the "false hyenas" of the genus *Percrocuta*. These elements joined other persisting Middle Miocene carnivores of Eurasian origin, such as the hypercarnivore amphicyonid *Agnotherium* and the ratel-like mustelid *Eomellivora*.

The persistence of forest conditions in this part of Africa is probably explained on the same basis as in southwestern Asia, that is, as a consequence of the monsoonal dynamics in this region. However, as happened in Siwaliks, a dramatic change is observed between 8 and 7 Ma in the mammalian communities of East Africa. At this time, there is a significant faunal turnover, involving the replacement of close to 75 % of the mammal species. Most of the old Middle Miocene holdovers are replaced by close relatives of the elements found today on the modern savannas. Therefore, this time records the first occurrence in Africa of leporids, hominids, new and extant viverrids, extant hienids, new felids, extant and diverse elephantids, new hippopotamids, extant giraffids, and several extant bovids. The former small- to medium-sized browser-based faunas are replaced by a new assemblage in which medium- to large-sized grazers, large browsers, and pursuit carnivores are dominant (Harris 1993).

This change parallels in many ways the one observed at the same time in the Siwaliks, when the former woodland biome opened and C_4 grasslands expanded over large parts of western Eurasia. Similarly, the period between 8 and 7 Ma records the expansion of the true savannas in the African continent, leading to the kind of open woodland and grasslands that are present in most of eastern and southern Africa. This is best exemplified by such latest Miocene faunas (Kerian) as Lothagam and Lukeino in Kenya or those of the Adu-Asa and the Sagantole Formations in Ethiopia. At Lothagam, recovery of more than 2,000 identifiable remains has produced a faunal list of more than 30 mammalian species (Leakey and Harris 2003). A number of new browsers replaced the medium-sized community of Middle Miocene origin, largely based on climacoceratid giraffoids and tragulids. Among them we find modern suids of the genera *Potamochoerus* and *Phacochoerus*, the peccary-like *Cainochoerus*, the tragelaphine antelope *Tragelaphus*, the black rhino *Diceros*, and the gomphotheres of the genus *Anancus*. These medium to large browsers joined a number of persisting elements that root in the former Sugutan faunas, such as the suids *Kubanochoerus* and *Nyanzachoerus*, the giraffid *Palaeotragus*, the bovids *Tragoportax* and *Sivatherium*, and the rhino *Brachypotherium*.

However, the most distinctive feature of the new fauna was the sharp increase in medium to large grazers, such as the large sivatherine giraffids of the genus *Sivatherium*; the first giraffines of the genus *Giraffa*; the elephantids *Stegotetrabelodon*, *Primelephas*, and *Elephas*; the modern hippos of the genus

Hexaprotodon; and the white rhino *Ceratotherium*. A new form of slender, grazer hipparionine horse, *Eurygnathohippus*, replaced the former mix-feeder *Hippotherium primigenium*. But the change to a grazer-dominated community is best exemplified by the bovids. Therefore, the new faunas include the first and abundant record of antelopes of the tribes Alcelaphini (*Damalacra*), Hippotragini (*Hippotragus*), Reduncini (*Kobus*, *Menelikia*), Aepycerotini (*Aepyceros*), and Antilopini (*Gazella*), which inhabit the present-day savannas.

The increase in diversity of large browsers and grazers led also to a change in the predator community. While the bear dog amphicyonids persisted, the number of pursuit carnivores suddenly increased. Thus, at Lothagam are represented several species of cursorial, wolflike hyenas (*Ictitherium*, *Hyaenictitherium*, *Hyaenictis*, *Ikelohyaena*), two species of machairodontine cats (*Lokotunjailurus*, *Dinofelis*), hunting viverrids (*Genetta*), and mustelids (*Ekoromellivora*, *Ekorus*).

Therefore, the change operated between 8 and 7 Ma from predominantly closed to predominantly open savanna environments led to a significant change in the mammalian communities, characterized by a dramatic increase in the number of medium to very large grazers, an increase in guild depth of large and very large browsers, and the presence of abundant and diverse pursuit carnivores (Harris 1993).

As evidenced by the Lothagam association, this is the environment where the first hominids succeeded. Besides a number of baboons (*Parapapio*, *Theropithecus*) and colobine monkeys (*Cercopithecoides*), Lothagam records the presence of an unidentified hominid, represented by some isolated teeth and a fragmented mandible. The site of Lukeino, dated between 6.2 and 5.6 Ma, also delivered remains of a hominid, *Orrorin tugenensis*, in a context that resembles that of Lothagam, with elephants (*Primelephas*, *Stegotetrabelodon*, *Loxodonta*), gomphotherids (*Anancus*), deinotheres (*Deinotherium*), rhinos (*Ceratotherium*, *Diceros*), chalicotheres (*Ancylotherium*), hipparions (*Eurygnathohippus*), hippos (*Hippopotamus*, *Hexaprotodon*), suids (*Nyanzachoerus*), giraffids (*Giraffa*), and a variety of antelopes: Cephalophini (*Cephalophus*), Reduncini (*Kobus*), Aepycerotini (*Aepyceros*), Tragelaphini (*Tragelaphus*), and Neotragini (Pickford and Senut 2001). The first hominids of the genus *Ardipithecus*, from the latest Miocene (5.7–5.5 Ma) of the Adu-Asa and Sagantole Formations in the Middle Awash, lived in a somewhat different environment (Wolde Gabriel et al. 2001). Although, as in Lothagam and Lukeino, large grazers are present (the elephants *Primelephas* and *Stegotetrabelodon*, the giraffid *Sivatherium*, the reduncine antelope *Kobus*, as well as hipparions), the dominance of browsing forms such as gomphotherids (*Anancus*), deinotheres (*Deinotherium*), rhinos (*Diceros*), hippos (*Hexaprotodon*), suids (*Nyanzachoerus*), and boselaphine and tragelaphine bovids (*Miotragocerus*, *Tragelaphus*) points to more wooded conditions.

Different again was the association found at Toros-Menalla 266, in Chad, dated between 7.4 and 5.2 Ma, where another early hominid species, *Sahelanthropus tchadensis*, was described (Vignaud et al. 2002). The faunal assemblage of Toros-Menalla shares with Lothagam and Lukeino the presence of a variety of large grazers: antelopes (*Kobus*, Hippotragini, Antilopini), elephants (*Loxodonta*), giraffids (*Sivatherium*), and hipparions (*Eurygnathohippus* cf. *abudhabiense*). However, the remaining association is based on medium to large browsers or mix feeders: *Anancus*, *Nyanzachoerus*, *Hexaprotodon*, and aff. *Palaeoryx*. Particularly surprising is the presence of the large, advanced anthracothere *Libycosaurus petrocchii* (also referred as *Merycopotamus petrocchii*), an element which is absent from the faunal associations of the same age in the eastern African basins. In fact, the Toros-Menalla 266 faunal assemblage fits better with the association found at the site of Sahabi (Libya), south of Benghazi.

The fauna from the Sahabi Formation (Boaz et al. 1987) shares a number of elements in common with the eastern basins, such as monkeys (*Macaca*, *Libypithecus*), archaic elephants (*Stegotetrabelodon*), rhinos (*Diceros*), hipparions (*Eurygnathohippus*), hippos (*Hexaprotodon*), tetraconodontine suids (*Nyanzachoerus*), giraffids (*Samotherium*), and a variety of antelopes: Reduncini (*Redunca*), Alcelaphini (*Damalacra*), Hippotragini (*Hippotragus*), and Antilopini (*Gazella*). However, a significant part of the association is composed of taxa that were common to the Greek-Iranian province and the Siwaliks region. This is the case, for instance, with the abovementioned anthracotherid *Libycosaurus* (related to *Merycopotamus*); the bovids *Miotragocerus*, *Prostrepsiceros*, and *Leptobos*; the amebelodontid gomphothere *Amebelodon*; and the whole carnivore taxocoenosis (*Machairodus*, *Chasmaporthetes*, *Hyaenictitherium*, *Adcrocuta*, *Indarctos*, *Agriotherium*; Howell 1987). In Sahabi, the botanical evidence provided by well-preserved fossil wood indicates an environment dominated by wooded savanna and semidesert grassland, with dominance of *Acacia* (64 %) and Mimosaceae (Dechamps and Maes 1987). The existence of periodic fires (a usual phenomenon in a savanna environment) is recorded as traumatic rings in fossil wood. The estuarine context of this site is reflected by the relative high proportion (13.5 %) of Salicaceae (*Populus euphratica*).

The western Asian character of the Sahabi fauna, which partly extends south to the Chad Basin (Toros-Menalla 266), opens the question of the origin of the Late Miocene African faunas, after the crisis at 7 Ma. It has been suggested that much of the current savanna fauna did not evolve in situ from the Early and Middle Miocene African mammals but migrated from more northern latitudes in the Late Miocene, replacing the previous forest endemic dwellers (Maglio and Cooke 1978). More specifically, with the drying out of Africa between 8 and 7 Ma, large mammals from the Greek-Iranian province may have colonized the lower latitudes, their adaptations to a sclerophyllous woodland (hypsodont teeth, cursorial skeletons) having acted as exaptations (sensu Gould and Vrba 1982) to a savanna biome (Solounias et al. 1999). This was probably the case for bovids, giraffids, equids, hyenas, rhinos, and hominids. The faunal composition of sites like Toros-Menalla and Sahabi strongly supports this scenario.

Conclusions

1. The Middle Miocene terrestrial ecosystems of western and central Europe were characterized by increasing levels of mammalian diversity of taxa associated with a woodland biome: proboscideans, chalicotherids, rhinoceroses, suids, cervids, tragulids, moschids, and hominoids; many of them were fruit eaters

and browsers. This high diversity of forest dwellers is also confirmed by the small mammal association, which includes eomyids, flying squirrels, dormice, and beavers. These high levels of diversity were probably a consequence of prevailing subtropical conditions.

2. In eastern Europe, however, we observe during the Middle Miocene a trend toward drier conditions, reflected in the abundance of hypsodont, grazing ruminants, mainly bovids and giraffids. This is the so-called Greek-Iranian Province, which extended from Greece to central Asia.
3. At the beginning of the Late Miocene (during the Vallesian Mammal Stage), diversity increased in Western Europe with the entry of new elements, like the hipparionine horses, giraffids, machairodont cats, ursids, and other eastern immigrants.
4. About 9.6 Ma, increasing seasonality and extension of deciduous forest led to the extinction of most of the browser taxa that had populated the Middle Miocene woodlands, such as suids, cervids, rhinoceroses, and hominoids (the so-called Vallesian Crisis). This loss of diversity is not clearly recognized in the Greek-Iranian Province, nor it is in western Asia, where a highly diversified mammalian fauna including hominoids is still present in the Siwaliks sequence.
5. However, worldwide extension of grasses at 7–8 Ma led to the final extinction of most of these elements in Eurasia, with the exception of eastern and southeastern Asia.
6. At this point, an extension to the south of the Greek-Iranian Province can be recognized. This led to the Plio-Pleistocene savanna biome, characterized by a high diversity of hypsodont bovids, large grazers like rhinoceroses and giraffids, and most probably the hominoids that led to the first hominins in Africa.

Cross-References

- ▶ Fossil Record of Miocene Hominoids
- ▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Postcranial and Locomotor Adaptations of Hominoids

Carol V. Ward

Contents

Abstract

Extant apes are adapted to various forms of below-branch forelimb-dominated arboreal locomotion and share morphologies associated with the shared aspects of their locomotor behaviors. With the expanding record of Miocene hominoid fossils, paleoanthropologists are coming to realize that although some shared characters may indeed be homologous, at least some almost certainly represent homoplasies. The apparently more primitive body plan of *Sivapithecus* than seen in Asian and African great apes indicates that at least some homoplasy has

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C.V. Ward (✉)
Department of Pathology and Anatomical Sciences, University of Missouri, Columbia, MO, USA
e-mail: wardcv@missouri.edu

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occurred within these clades. Furthermore, the expanding fossil record may be indicating a greater diversity of positional behaviors within the Hominoidea than previously appreciated; for example, *Pierolapithecus* has been argued to indicate the evolution of suspensory locomotion in combination with arboreal quadrupedalism, and *Nacholapithecus* is unique with its enlarged forelimb but otherwise primitive body plan. These new fossils reveal that variation is prevalent and critical to appreciate for reconstructing hominoid evolutionary history. Furthermore, it seems increasingly likely that many postcranial and locomotor specializations of great apes may have evolved from ancestors that were more generalized than are living hominoids. This realization is critical for interpreting the ancestral morphology from which hominins were derived.

Introduction

One of the most distinctive shared characteristics of modern apes is their specialization for below-branch forelimb-dominated arboreal locomotion, many adaptations for which are still seen in humans today (Huxley 1863; Keith 1923). Extant apes all exhibit an overlapping set of adaptations to suspension and orthograde climbing in their torsos, limbs, hands, and feet. They have elongated forearms and hands; high-intermembral indices; laterally oriented shoulder joints; limb joints adapted to loading in a variety of postures; short, broad torsos; and absence of a tail. Given this suite of apomorphies, parsimony would seem to dictate that ancestral apes should have been suspensory as well (Gregory 1916). If not, extant hominoids must have developed these adaptations independently, which would, on the face of it, seem to involve an unlikely amount of homoplasy.

However, while below-branch forelimb-dominated arboreality distinguishes all modern ape taxa from other catarrhines (Schultz 1930, 1969a, b), it is not a monolithic adaptation (Larson 1988). Young (2003) has suggested that great ape postcranial adaptations are homologous (see also Pilbeam 2002) and that hylobatids may be autapomorphic, due to their small size and exclusively arboreal specialization for brachiation that involves moving rapidly through the trees in ricochetal fashion. Yet arboreal adaptations actually vary among extant ape genera more than is often emphasized in considerations of the evolution of hominoid locomotion, reflecting specialization on different types and amounts of climbing and suspensory behavior. Orangutans almost never use the ground, yet, given their large body size, they move cautiously through the upper levels of the canopy with quadrumanous climbing and arm hanging. Their forelimbs are astonishingly long and all joints are flexible and employed in diverse postures (MacKinnon 1974; Cant 1987).

Chimpanzees, arboreal when foraging, hunting, and sleeping, spend much of their time as terrestrial knuckle walkers (Goodall 1965; Hunt 1990), as do bonobos, although the locomotor behavior of the latter is less well studied (Doran 1993). Gorillas are extremely large and are even more terrestrial than chimpanzees or bonobos, yet particularly in certain habitats they habitually climb trees frequently for feeding and sleeping (Tuttle and Watts 1985; Remis 1995). Hominins, of course, modified their locomotor skeletons to specialize in the most distinctive of all primate locomotor behaviors, habitual terrestrial bipedality, although they likely evolved from ancestors that were at least somewhat adapted to climbing or suspensory arboreal locomotion. Given this variation among taxa, a certain level of independence in the acquisition of some suspensory traits should perhaps not be considered entirely unlikely.

The burgeoning fossil record is strengthening the hypothesis that climbing and suspensory adaptations developed in mosaic fashion over evolutionary time and occurred in different ways and even multiple times in separate hominoid lineages (Sarmiento 1987; Pilbeam et al. 1990; Moyà-Solà and Köhler 1995; Begun et al. 1997; Finarelli and Clyde 2004; Moyà-Solà et al. 2004; Crompton et al. 2008; Lovejoy et al 2009; Almécija et al. 2013; Hammond et al. 2013). Timing of wrist bone development differs among chimpanzees and gorillas, also suggesting some homoplasy even between these taxa (Kivell and Schmitt 2009). The hominoid fossil record now includes over 28 genera known from as early as 20 Ma, and many taxa are known from postcranial elements (see Hartwig 2002; Begun et al. 2012). Among these fossil taxa, there is much wider range of known locomotor modes than among extant ones. Adaptations seen in some, and even all, extant apes do not occur as a block. For example, *Nacholapithecus* has elongated forelimbs but a long, narrow torso and apparently pronograde quadrupedal posture (Rose et al. 1996; Senut et al. 2004; Ishida et al. 2004). *Pierolapithecus* has what appears to be a hylobatid-like torso structure, yet does not seem to have particularly long digits (Moyà-Solà et al. 2004; Hammond et al. 2013). Considering variation within living and fossil hominoids may lead us away from dichotomous views on whether the euhominoid ancestor was "great apelike" or "basal hominoid-like" (Pilbeam et al. 1990; Young 2003; Crompton et al. 2008) and may lead us to a more nuanced and more accurate understanding of how hominoids evolved.

The positional behavior variation among extant and fossil hominoids provides an important set of information about hominoid phylogeny and evolution. This chapter will summarize the postcranial adaptations of extant and the best-known fossil hominoid genera and put these taxa into phylogenetic context in order to explore evolutionary patterns in hominoid postcranial and locomotor adaptations.

Extant Hominoids

Living apes all share a suite of adaptations to below-branch, forelimb-dominated arboreality, although they do not exploit this locomotor niche identically and are distinguishable postcranially, although particularly among great apes differences are poorly characterized (Young 2003; but see Larson 1988; Inouye and Shea 1997; Drapeau 2001). All, though, have evolved to negotiate terminal branches of arboreal substrates by hanging below branches and distributing their weight among multiple supports. Their relatively large body sizes and long forelimbs allow them to bridge gaps in the canopy rather than leaping. They lack tails, which are no longer necessary for balance within this type of locomotor regime. As a consequence, the musculature usually associated with tails in nonhominoid primates has become restructured to form a muscular pelvic floor, providing support for the viscera during the orthograde postures common in all ape species today (Elftman 1929).

Apes have high-intermembral indices (Schultz 1930; Aiello 1981; Jungers 1985). When climbing, their long forelimbs and relatively short hindlimbs improve their ability to negotiate large-diameter vertical supports. The long arms also assist in increasing their reach for bridging gaps and grasping branches. Limb proportions vary however (Aiello 1981; Jungers 1984, 1985). Orangutans and hylobatids have proportionally longer forearms and hands than do chimpanzees, and chimpanzees and bonobos alone have differentially elongated metacarpals more than other extant apes (Drapeau 2001).

Ape torsos are broad, with the scapulae positioned dorsally and glenoid fossae oriented laterally (Keith 1923; Schultz 1930, 1961, 1969a; Benton 1965, 1976; Sarmiento 1987; Ward 1993). Their ribs have higher costal angles, sterna are broad, scapulae have a cranially oriented glenoid fossa, and their clavicles are long (Schultz 1937; Cartmill and Milton 1977; Larson 1993). The broad torso and wide pectoral girdle results in a shoulder position that places the scapulothoracic musculature more in the coronal plane, facilitating adduction of the upper limb (Erickson 1963; Benton 1965, 1976; Ward 1993). Adduction is accomplished primarily by the *latissimus dorsi* muscle along with others that are important in hoisting the body up from an arm-hanging position and in pulling the body among supports in the trees (Swartz et al. 1989; Hunt 1991). Extant hominoid pectoral girdle form also increases the reach of the forelimbs and circumduction at the shoulder (Cartmill and Milton 1977).

Extant hominoid lumbar spines are reduced in length, with only 5–6 lumbar vertebrae in lesser apes, compared with the typical primate number of 7, and great apes have only 3–4, so that the lower ribs approximate the iliac crest (Schultz and Straus 1945; Erickson 1963; Ankel 1967, 1972; review in Ward 1993). African apes differ from humans, orangutans, and hylobatids in having 13 rather than 12 thoracic vertebrae and ribs (Schultz 1930, 1969a, b). This variation in thoracic vertebral count among extant hominoids is noteworthy and may be yet another small line of evidence supporting hypotheses of postcranial homoplasy among extant apes. All great ape lumbar spines are almost completely inflexible (Slijper 1946; Schultz 1969a, b; Benton 1976). Their iliac blades are craniocaudally elongated, expanding the distance between hip and sacroiliac joints (Waterman 1929; Ward 1993). Part of *latissimus dorsi* inserts directly upon the iliac crest (Sonntag 1923, 1924; Waterman 1929; Gregory 1950). The reduced lumbar spine provides a stiffer platform for these muscles to act upon the upper limb and protects the vulnerable lumbar spine from excessive lateral bending moments during latissimus dorsi contractions (Cartmill and Milton 1977; Jungers 1984; Sarmiento 1985; Ward 1993).

Reaching overhead during climbing requires the ability to adduct the wrist, which apes can do due to a reduced ulnar styloid that has lost contact with the carpus (Lewis 1971, 1972, 1989; Sarmiento 1988; Whitehead 1993). The pisiform is more distally situated, facilitating extensive adduction at the wrist up to 90° (Sarmiento 1988). Apes rely on a hook grip during suspensory behaviors and have relatively long fingers with strong flexor musculature and reduced thumbs (Schultz 1930; Rose 1988). They also have strong grasping *pollices* and *halluces*, along with well-developed musculature for adduction. The fibula, site of attachment of the long hallucal flexor muscles, is well developed (Schultz 1930; Sonntag 1923, 1924; Gregory 1950; Swindler and Wood 1973). Manual and pedal phalanges have well-developed attachment sites for digital flexors (review in Begun 1994a). The curved forearm bones of apes have been linked to the presence of strong hand and finger flexors (Miller 1932; Knussmann 1967).

These adaptations are better developed in great apes than in lesser apes (review in Young 2003). Mechanical constraints on mechanical function, and stresses on the musculoskeletal system, increase exponentially with increasing body size; thus some differences between lesser and great apes may represent allometric issues (Aiello 1981; Jungers 1984). The small body size of hylobatids may be secondarily derived, as is their unique adaptation for ricochetal brachiation (Cartmill 1985). Their fore-limbs and hands are particularly elongate (Jungers 1984), their thumbs particularly short, and their body mass relatively low. Their lumbar vertebral columns are 5–6 segments long and their thoracic columns 12 (Schultz and Straus 1945).

Differences between African apes and orangutans have also been noted, including a smaller supraspinous region of the scapula, smaller acromion processes, and shorter scapulae in orangutans (Oxnard 1984; Larson 1988; Young 2003). Orangutans have higher intermembral indices (Aiello 1981), a nonuniformly curved iliac crest, and an anterior longitudinal ligament ridge on the anterior surfaces of the vertebral bodies. They also lack a ligamentum teres of the femoral head, along with particularly mobile knee and midtarsal joints. Orangutans alone among large hominoids retain separate centrale and scaphoid bones rather than the fused os centrale seen in extant African apes. These differences are presumably related to the highly developed and nearly exclusively quadrumanous arboreal locomotor behavior of orangutans on one hand compared with the partly terrestrial knuckle-walking habits of African apes on the other. It is worth noting, however, that little work has been done to explore the extent of morphological variation among great apes and their functional significance.

So, although apes do share a distinctive suite of morphologies, they are not identical in their behavior nor anatomy. Therefore, although a subset of shared morphologies undoubtedly was present in their common ancestor and represents synapomorphies of the hominoid clade, such differences indicate a combination either of locomotor specialization within each lineage or independent acquisition within lineages undergoing broadly similar selective pressures. Only careful examination of the currently known fossil record, and discovery of new hominoid fossils, will allow us to determine which scenarios led to the diversity of known hominoid locomotor adaptations.

Fossil Non-hominin Hominoids

Hominoids can essentially be grouped into temporal and adaptive grades, basal hominoids, and euhominoids (Begun et al. 1997, 2012; Begun 2010; Begun 2001) (Fig. 1). Basal hominoids are stem taxa known from the Early and Middle Miocene

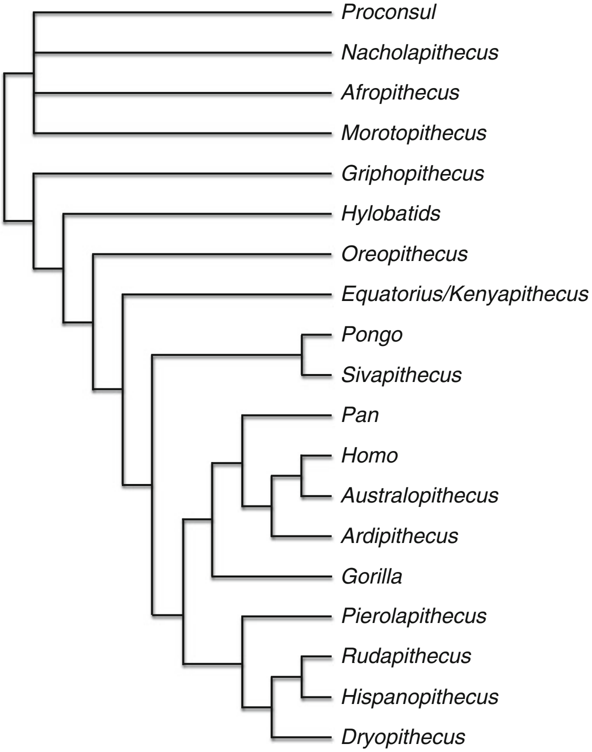

Fig. 1 Hypothesized phylogeny of hominoid relationships (based on Begun et al. 2012) followed in this chapter

and comprise taxa that are not crown hominoids and that lack postcranial specializations for extant apelike below-branch arboreality. Euhominoids are members of a crown hominoid clade, and so demonstrate extant hominoid synapomorphies, of which the postcranial anatomy is significant to this discussion. In an analysis of relatively well-known taxa (Begun et al. 1997), basal hominoid taxa include *Proconsul* and *Afropithecus* from the Early Miocene and *Kenyapithecus*, which in the analysis includes *Equatorius* (Ward et al. 1999), *Griphopithecus* (Begun 2000) from the Middle Miocene, and to which should now be added *Nacholapithecus* from the Middle Miocene (Ishida et al. 1984, 2004; Rose et al. 1996; Nakatsukasa et al. 1998). Euhominoids include *Sivapithecus*, *Oreopithecus*, *Pierolapithecus*, *Rudapithecus*, *Hispanopithecus*, and *Dryopithecus*

Proconsul and *Afropithecus*

Postcranially the best-known genus of Early Miocene hominoid is *Proconsul*, although *Afropithecus* is also represented by several postcranial elements. While these taxa differed craniodentally, *Afropithecus* is strikingly similar in preserved postcranial bones to *Proconsul nyanzae* (Ward CV1998). These taxa, among others less well known postcranially, represent a stem group referred to as basal hominoids

(Begun et al. 1997). Comprehensive reviews of these taxa can be found in Walker (1997) and Leakey and Walker (1997), and possibly *Nakalipithecus* (Kunimatsu et al. 2007), *Ouranopithecus* (Andrews et al. 1996; Moyà-Solà and Köhler 1995; de Bonis and Koufos 2001) and *Chororapithecus* (Suwa et al. 1997), but without good postcranial representation, these latter taxa are not discussed further here.

Proconsul was a genus composed of at least four species of pronograde, quadrupedal, arboreal frugivores that ranged in size from that of colobus monkeys to that of female gorillas. *Proconsul* individuals were very generalized animals. They were certainly above-branch arboreal quadrupeds that would have been capable, as most primates are, of limited below-branch postures and movement but that show no specialization for below-branch arboreality. *Proconsul* had a roughly even intermembral index and retained ulnar contact with the wrist (Beard et al. 1986). It also had a relatively long torso with six lumbar vertebrae, lacking the stiffening of the lumbar spine seen in extant apes (Ward 1993; Ward et al. 1993). The vertebrae have transverse processes arising from the vertebral body as in most monkeys, distinct accessory processes that suggest large *erector spinae* musculature, reflecting a narrow rib cage, and narrow and laterally facing iliac blades (Ward 1993). The pelvis was narrow, as, presumably, was the thoracic cage. The humerus is retroflexed with little torsion, reflecting ventrally oriented glenohumeral joints (Napier and Davis 1959; Larson 1988). The sternebrae are wider than those of cercopithecids, instead resembling atelines, but were not as broad as those of apes.

Proconsul is distinguished postcranially from earlier generalized catarrhines such as *Aegyptopithecus* (Rose 1997; Walker 1997) by a shoulder adapted to a wider range of loading, an elbow joint emphasizing joint loading in a variety of flexion-extension and pronation-supination postures, longer distal limb segments, a foot that may have been better adapted to inversion-eversion (Walker 1997, Table 1 p. 221), and the lack of a tail (Ward et al. 1991; Nakatsukasa et al. 2004). It is also true that *Proconsul* had a hip joint with a high neck-shaft angle, a femoral head set high on the neck, a centrally placed fovea capitis, and a greater trochanter that was shorter than that of many monkeys, indicating a hip joint adapted to loading in at least somewhat abducted postures (Ward 1992; Ward C 1997), although not necessarily with a greater range of possible abduction than found in most monkeys (Hammond 2013). The knee joint was broad, with a broad, flat patella, also indicating a very generalized and adaptable use of the lower limb. Most monkeys and earlier, generalized catarrhines have joints designed for fairly stereotypical loading environments principally comprising of quadrupedal postures in which the limbs are relatively adducted and the hands are pronated and palmigrade. Thus in comparison to *Aegyptopithecus*, *Proconsul* and other known Early Miocene basal hominoids were adapted for using their limbs in more abducted postures, with hands and feet grasping arboreal supports in a variety of positions.

The hands and feet of *Proconsul* have relatively well-developed first rays and supporting bones such as the large fibula. The phalanges are fairly long, with clear ridges for attachment of the finger and toe flexors (Begun 1993). The hallux and pollex were long relative to the other digits, suggesting that actual grasping was used rather than emphasizing the hook grips characteristic of extant apes.

Before the discovery of taillessness in *Proconsul*, reduction of a tail and commensurate restructuring of the pelvic floor musculature had been equated with the evolution of orthograde posture, which requires muscular support of pelvic viscera. However, the lack of a tail in *Proconsul*, and also in *Nacholapithecus* (Ward et al. 1991; Nakatsukasa et al. 2004), reveals that tail loss in hominoids was not associated with orthogrady, but rather with a decreased reliance on running and leaping behaviors and an emphasis on more deliberate arboreality, emphasizing manual and pedal grasping with weight distributed over multiple supports (Kelley 1995). Taillessness was likely a characteristic of all basal hominoids and one of the defining features of this superfamily.

In summary, a reasonable locomotor reconstruction of early hominoids is possible. The positional repertoire of the earliest known hominoids likely was distinguished from that of primitive catarrhines such as *Aegyptopithecus* by a specialization for deliberate arboreal climbing and clambering, using strong manual and pedal grasping to maintain balance and to move about in the arboreal environment. The emphasis on grasping meant that tails were no longer needed for balance, and thus an external tail became lost. A grasping adaptation enabled many hominoids to attain larger body sizes than seen in extant monkeys, yet still remain arboreal. This emphasis on cautious climbing and clambering enabled basal hominoids to reach fruit on the terminal branches and cross gaps in the canopy by giving them the ability to distribute their weight over multiple supports. They almost certainly also practiced vertical climbing and limited suspension but had not yet evolved selection for specialized adaptations to these behaviors; instead they spent most of their time above the branches. Their limb joints were adapted to loading in a wider variety of postures than is typical for most nonhominoids, including those involving an abducted hip and supinated elbow. They were certainly capable of orthograde postures and probably employed them often. Yet their narrow torso structure with ventrally oriented shoulder joints and ulnocarpal contact that limited ulnar deviation of the wrist indicate locomotion primarily with the limbs positioned mainly underneath the body or slightly abducted.

This generalized arboreal locomotor habitus permitted this early radiation of basal hominoids to exploit a variety of body sizes, as well as a breadth of ecological niches. *Proconsul* was likely a ripe-fruit frugivore and *Afropithecus* a seed predator (Leakey and Walker 1997). *Rangwapithecus*, less known postcranially, seemed to be at least partly folivorous (Kay and Ungar 1997). Thus, except for *Morotopithecus* (below), Early Miocene apes seem to be an adaptive radiation that shared a broadly similar set of locomotor adaptations.

Morotopithecus

Morotopithecus bishopi is the earliest Miocene ape known from eastern Uganda and dated at over 20.6 Ma (Gebo et al. 1997). The palate of this taxon resembles those of other basal hominoids and has been compared to both *Proconsul* (*P. major*) and *Afropithecus* (review in Leakey and Walker 1997). As such, this species is placed phylogenetically as a basal hominoid rather than as a euhominoid. Postcranially, however, it differs from other Early Miocene apes in displaying a more derived, modern apelike postcranial skeleton in some respects. The only postcranial elements known from *Morotopithecus* include a glenoid fossa, a lumbar vertebra and associated fragments of other lower vertebrae (Walker and Rose 1968), and partial femora.

The *Morotopithecus* glenoid fragment is similar to its counterpart in extant great apes, being ovoid and shallow and lacking a narrow, laterally concave cranial portion (MacLatchy et al. 2000). This suggests a shoulder joint adapted to loading in a variety of postures and may be associated with a broader upper torso morphology. A more extant apelike torso in *Morotopithecus* compared with *Proconsul* is also suggested by the lumbar vertebrae (Ward 1993; Sanders and Bodenbender 1994; Nakatsukasa 2008), which are morphologically similar to those of hylobatids in having short bodies relative to endplate dimensions (Nakatsukasa 2008) and have lumbar vertebral transverse processes which arise from the junction of the vertebral body and pedicle (Walker and Rose 1968) rather than from the body as in *Proconsul* (Ward 1993; Ward et al. 1993) or *Nacholapithecus* (Nakatsukasa et al. 1998; Nakatsukasa 2008). This is correlated with the lack of accessory processes (Ward 1993). The body is also not hollowed out laterally, although a rounded median keel or bulge (Nakatsukasa 2008) is present. The *Morotopithecus* femur is robust, with a small head, but displays the typical hominoid pattern of having a high neck-shaft angle and centrally placed fovea capitis. The distal femur is very broad mediolaterally, with condyles asymmetric in size, and there is a large popliteus groove as in extant apes, suggesting adaptation to habitual loading in a variety of postures, and a high degree of rotation of the knee joint. Still, *Morotopithecus* may have had more lumbar vertebrae than typical great apes based on additional vertebral fragments from the site showing more ventral wedging of the vertebral bodies than typical for great apes, variable placement of the transverse processes relative to the vertebral body and pedicle (Nakatsukasa 2008), and mediolaterally narrow laminae. This suggests that the overall vertebral column was not as derived as seen in extant apes.

Altogether *Morotopithecus* shares several key features with extant apes, suggesting adaptation for more below-branch arboreal activities. The shoulder, hip, and knee appear to suggest adaptation to a variety of postures, and the vertebrae suggest a certain amount of broadening and stiffening of the torso, but not perhaps as much as in extant great apes at least. There is also nothing in the *Morotopithecus* skeleton that is substantially more derived than that of hylobatids except for a broader knee joint and the presence of a gluteal ridge and perhaps also transverse process inclination (Young and MacLatchy 2004). The femoral characters may be related to body size variation, and the transverse process inclination is actually somewhat intermediate between that of gibbons and great apes (Shapiro 1993). Still, the hominoid similarities have led MacLatchy (2004), MacLatchy et al. (2000), and Young and MacLatchy (2004) to hypothesize that *Morotopithecus* is a basal member of the euhominoid clade and that other basal hominoids, like *Proconsul*, *Afropithecus*, *Nacholapithecus*, and *Equatorius*/*Kenyapithecus* at least, are more distantly related to extant apes. This hypothesis assumes that the postcranial adaptations shared by extant hominoids in torso restructuring, below-branch locomotion, and knee mobility are synapomorphies.

Given its primitive craniodental and perhaps some vertebral characters, the phylogenetic placement and thus the evolutionary implications of *Morotopithecus* are difficult to assess. But considering the homoplastic similarities between ateline monkeys, *Pliopithecus*, and extant hominoids, and the variation among extant hominoids, it certainly seems plausible that shared features of *Morotopithecus* and great apes represent homoplasies. Regardless of its phylogenetic affinities, it seems apparent that *Morotopithecus* was a more forelimb-dominated below-branch arboreal animal with a greater emphasis on orthograde postures than is typical for other basal hominoids.

Nacholapithecus

Nacholapithecus kerioi is a Middle Miocene ape from northern Kenya (Ishida et al. 1984, 2004; Pickford et al. 1987; Rose et al. 1996; Nakatsukasa et al. 1998; Nakatsukasa 2003a, b). It displays an unusual suite of morphologies in a very different combination than known for other hominoids. Its overall body plan is similar to that of *Proconsul*. It has a long vertebral column with six lumbar vertebrae shaped like those of *Proconsul* (Nakatsukasa et al. 1998). It appears to have had a narrow torso shape and no tail, yet its feet were long, its shoulder joints mobile, and its upper limbs very large (Nakatsukasa et al. 1998; Senut 2003; Ishida et al. 2004). The hands and feet reflect palmigrade, plantigrade quadrupedalism.

The body proportions of *Nacholapithecus* are striking, having very large forelimb and relatively small hindlimb elements, outside the observed ranges for even extant apes (Ishida et al. 2004). The lower limb is comparatively small, but there is a high neck-shaft angle of the femur and a short neck. Otherwise, the tibia, fibula, and tarsal bones are similar to those of *Proconsul*. What is different are the very long pedal digits found in *Nacholapithecus*, which are similar in size to those of chimpanzees despite the fact that it is thought to have weighed about half of what chimpanzees weigh (22 kg; Ishida et al. 2004). The ribs are relatively large, and it has a long clavicle and scapular spine (Ishida et al. 2004; Senut et al. 2004; Nakatsukasa et al 2007). The distal humerus is derived relative to that seen in *Proconsul*, with a better-developed ball-and-socket morphology of the humeroradial joint and a more symmetrical humeroulnar joint. It had a relatively long clavicle with ligament markings, suggesting that protraction of the humerus into overhead postures would have been emphasized rather than abduction (Senut et al. 2004). The morphological similarity between the shoulder bone morphologies and those of colobine monkeys underscores this interpretation. This difference in inferred upper limb use in climbing between *Nacholapithecus* and euhominoids is likely related to its lack of torso restructuring from the primitive condition. *Nacholapithecus* retained six or seven lumbar vertebrae with ventral median keels and hollowed sides, transverse processes arising from the body-pedicle junction, and small accessory processes are present as in *Proconsul*

(Nakatsukasa et al. 2007). This restructuring to make the torso shorter, stiffer, and broader is seen in apes emphasizing abduction-adduction movements of the upper limb (Ward 1993). This is consistent with the caudal orientation of the spinous processes in the lower thoracic and lumbar vertebrae as well (Nakatsukasa et al. 2007). Thus, *Nacholapithecus* does seem to have been adapted for more extensive forelimb-dominated climbing locomotion than were earlier basal hominoids, with enlarged forelimbs and small hindlimbs and long pedal phalanges, but in a fundamentally different way from what is seen in later euhominoids.

Equatorius/Kenyapithecus

The Middle Miocene African fossil sample originally attributed to *Kenyapithecus* has now been partly divided by some researchers and placed into *Equatorius* (Ward et al. 1999) or *Griphopithecus* (Begun 2000), with the result that there is now only one humerus known for *Kenyapithecus wickeri* (summary by Ward and Duren 2002). Given the taxonomic debate, here all samples are treated together.

Equatorius resembles other basal hominoids in several respects (Sherwood et al. 2002). It has a monkey-like scapula and a retroflexed humeral shaft, indicating a pronograde posture at the shoulder. The ulna still contacts the carpus, and the os centrale is unfused to the scaphoid. *Equatorius* has the mobile hip and knee joint morphology characteristic of all hominoids and slightly broader sternebrae than typical for monkeys, although it is reconstructed to lack the laterally expanded torso of extant apes. *Equatorius* (= *Kenyapithecus*) from Maboko Island has been interpreted as semiterrestrial based on its retroflexed humeral shaft, medial humeral epicondyle, and olecranon process, along with long radial head, short phalanges, and morphology of the metacarpal heads (McCrossin and Benefit 1997). However, it has also been described as resembling extant apes in having a straight humeral shaft and strong grasping capabilities (McCrossin 1997). It is difficult to reconcile these divergent descriptions at present. *Equatorius* does not display evidence of thoracic reorganization typical of *Morotopithecus* or extant apes, but instead was a more generalized pronograde quadruped that may have spent some time on the ground. If indeed *Equatorius/Kenyapithecus* is more closely related to euhominoids than is *Proconsul* (Ward and Duren 2002), it reinforces the hypothesis that the ancestral euhominoid was generalized postcranially.

Griphopithecus

Griphopithecus is known from the early Middle Miocene of central and eastern Europe and Turkey. Postcranially, phalanges from the site of Paşalar, Turkey, are fairly short and straight, lacking evidence of climbing adaptations (Ersoy et al 2008). A partial ulna and humerus from Kleinhadersdorf, Austria, also appear to be those of a generalized quadruped (Begun 2002; Alba et al. 2010).

Sivapithecus

Sivapithecus is known from more than one species from the Middle and Late Miocene of Pakistan. It shares an extensive suite of craniodental characters with orangutans, suggesting that they are sister taxa. Postcranially, however, these taxa are not similar. The discovery of humeral shafts attributed to *Sivapithecus* (Pilbeam et al. 1990) led to a startling revelation about the evolution of hominoid locomotion, referred to as the "*Sivapithecus* dilemma" by Pilbeam and Young (2001). The hand and foot remains known for *Sivapithecus* up to that time all exhibited a more derived modern apelike morphology than earlier hominoids such as *Proconsul*. It had longer, stronger phalanges, a better-developed hallux, and a more mobile elbow, and these morphologies were presumed to indicate at least a somewhat extant great-apelike overall postcranial gestalt (Rose 1986). To most researchers the marked craniofacial similarities between *Sivapithecus* and *Pongo* indicate a close phylogenetic relationship (Ward and Brown 1986; Ward SC 1997; Kelley 2002; Begun 2010; Alba et al. 2012), so the apparently modern apelike postcranial fossils fit a phylogenetic position of *Sivapithecus* well within the hominid clade.

The humeri, however, appear to paint a different picture. Although missing their proximal ends, both specimens appear to be inclined posteriorly and medially, the morphology seen in primates like most monkeys, *Proconsul*, and *Nacholapithecus* that have posteriorly directed humeral heads, ventrally facing scapular glenoid fossae, and narrow torso structures (Pilbeam et al. 1990; Richmond and Whalen 2001; Madar et al. 2002; Almécija et al. 2007; Desilva 2010).

If *Sivapithecus* had a narrow torso, and yet was a member of the pongine clade, this means that many of the postcranial apomorphies shared among *Pongo*, *Pan*, and *Gorilla* must represent homoplasies rather than homologies as previously interpreted. *Pongo* must have evolved a similar torso structure, limb proportions, and other below-branch specializations independently from African apes. This presented paleoanthropologists with the initially uncomfortable realization that the unique locomotor mode essentially shared by extant apes evolved independently, at least twice.

Pierolapithecus

The hypothesis that postcranial homoplasy has occurred among extant hominoids is bolstered by the recent discovery of *Pierolapithecus catalaunicus* from the Middle Miocene of Spain (Moyà-Solà et al. 2004). *Pierolapithecus* was originally interpreted as a basal hominid (Moyà-Solà et al. 2004; 2009; Casanovas-Vilar et al. 2008, 2011) but has also been considered a member of the hominine (African ape and human) clade (Begun and Ward 2005; Begun 2009; Begun et al 2012). The vertebrae of *Pierolapithecus* resemble those of *Morotopithecus* and, among extant apes, are most like those of hylobatids. It had a high costal angle, revealing that its torso shape was also hominoid-like. It lacked ulnar contact with the carpus, indicating the ability for substantial ulnar deviation. All of these features are also seen in extant hominoids and suggest an orthograde locomotor adaptation involving some climbing at least.

However, *Pierolapithecus* is more primitive than are extant apes in some ways. It lacks some shared specializations of extant great apes, such as dorsally positioned vertebral transverse processes, elongated curved phalanges, some reorganization of the carpus, or a flaring iliac blade as seen in large hominoids (Almécija et al. 2009; Moyà-Solà et al. 2004; Alba et al. 2010; Hammond et al. 2013). Still, the vertebrae and pelvic fragment appear to resemble those of hylobatids, which are highly suspensory, and the phalanges are similarly curved to those of chimpanzees, so some features in which the morphology does not resemble all great apes may not mean lack of orthograde or even suspensory behaviors. Too few elements are known from both *Sivapithecus* and *Pierolapithecus* to make extensive direct comparisons, so it is hard to say if they represent an ancestral morphology from which all extant apes evolved. But, because it lacks some of the shared specializations of extant great apes, *Pierolapithecus* provides more evidence that *Pongo* is convergent upon African apes in its specialized below-branch arboreal locomotor skeleton.

Oreopithecus

Oreopithecus bambolii is a Late Miocene ape from Italy represented by a deformed but nearly complete skeleton, as well as other isolated postcranial elements. It is known from most skeletal elements and has been the subject of intense debate regarding its locomotor behavior (Schultz 1960; Harrison 1986; Sarmiento 1987; Harrison and Rook 1997; Pilbeam 2004; Moyà-Solà et al. 1999; Rook et al. 1999). It has even been considered to be bipedal (Straus 1963; Köhler and Moyà-Solà 1997; Moyà-Solà et al. 1999, 2005; Rook et al. 1999; Macchiarelli et al. 2001), although its vertebral anatomy does not support this hypothesis as the lumbar vertebrae lack dorsal wedging and a caudal increase in interfacet distances (Russo and Shapiro 2013). Furthermore, many of the features argued to suggest bipedality are also found in suspensory mammals (Wunderlich et al. 1999).

Oreopithecus has extremely high-intermembral and brachial indices, resembling only those of orangutans. It has five lumbar vertebrae, as do humans and hylobatids, but without a lumbar lordosis (Russo and Shapiro 2013). It had a pelvis that is broader than those of hylobatids with enlarged anterior inferior iliac spines. Its upper thoracic and pectoral girdle morphology is more difficult to assess due to the crushing experienced by the published fossil bones. *Oreopithecus* also has a relatively large femoral head relative to neck size, associated with extensive hip joint mobility (Ruff 1988). It was clearly adapted for below-branch arboreality, although its metacarpals and phalanges are not particularly long (Moyà-Solà et al. 1999; Rook et al. 1999), perhaps suggesting that manual grasping was done between the pollex and medial digits rather than with the hook grip typical of extant apes. This would be yet another example of variations on the below-branch forelimb-dominated theme. *Oreopithecus* also demonstrates that hominoids can specialize in this type of locomotor behavior without having every specialization seen within any given extant ape taxon. Because of its apomorphic craniodental morphology, the phylogenetic position of *Oreopithecus* is debated (Harrison and Rook 1997; Begun et al. 2007; Begun 2009, 2010; Casanovas-Vilar et al. 2011), but it is considered to be a crown hominoid and probably a basal one (Begun et al. 2007; Begun 2009, 2010; Casanovas-Vilar et al. 2011). Thus, its clear adaptation to orthogrady supports the hypothesis that euhominoids were orthograde at least by the Middle Miocene in Europe, although its unusual morphology and unusual environment suggests that some of its extreme suspensory adaptations may represent homoplasies with extant large hominoids.

Dryopithecus

Miocene ape fossils from Spain, France, and Hungary until recently were all referred to the genus *Dryopithecus* but now are recognized as belonging to the distinct genera *Dryopithecus*, *Hispanopithecus*, and *Rudapithecus* (recent review in Begun et al. 2012). *Dryopithecus fontani* from the Middle Miocene of Spain and France is known postcranially only from some phalanges (Almécija et al. 2011), a proximal femur (Moyà-Solà et al. 2009; Alba et al. 2010; Pina et al. 2011), and two humeri (Lartet 1856; Alba et al. 2010; Alba et al. 2012). *Dryopithecus* does not appear to have been well adapted for suspensory behaviors, differing from extant apes in having a lower femoral neck-shaft angle and higher trochanter and somewhat curved humeri resembling those of quadrupedal catarrhines.

Hispanopithecus

Hispanopithecus catalaunicus is a Late Miocene euhominoid from Spain that appears to have among the most derived postcranial skeleton of any Miocene ape (Begun 1993, 1994b; Moyà-Solà and Köhler 1996; Almécija et al. 2007, 2009; Alba et al. 2012).

Hispanopithecus has dorsally positioned lumbar transverse processes that arise from the neural arch and are inclined posteriorly, although not as far as in extant great apes (Moyà-Solà and Köhler 1996). Its robust femur has a high neck-shaft angle and low trochanter, suggesting adaptation to using the hip in a variety of postures and in many respects is similar to that of orangutans (Köhler and Moyà-Solà 1997), and an extant apelike distribution of bone in its femoral neck (Pina et al. 2012). It is not possible to determine how many were originally present. It has long, powerful manual phalanges coupled with short, robust metacarpals and limb proportions similar to those of modern chimpanzees and bonobos (Moyà-Solà and Köhler 1996; Almécija et al. 2007, 2009; Alba et al. 2012; Pina et al. 2012). The ulna did not contact the wrist (Begun 1994b; Moyà-Solà and Köhler 1996), and the forelimb bones are elongate. Altogether, *Hispanopithecus* appears to have been orthograde and more highly suspensory than earlier Miocene apes.

Rudapithecus

Rudapithecus hungaricus is a Late Miocene ape from Hungary that also is a member of the crown hominid clade. Like *Hispanopithecus*, *Rudapithecus* appears to have had numerous adaptations to suspensory behavior. It has long, curved manual phalanges, although these are less robust than seen in *Hispanopithecus* (Begun 1992, 1993; Kivell and Begun 2009; Begun et al. 2012). The elbow shows signs of considerable mobility, and the femur is short with a large head, as in extant great apes (Begun et al. 2012). The wrist has no contact with the ulna, and there was a deep carpal tunnel suggesting powerful forearm flexors. *The Rudapithecus* scaphoid and capitate anatomy is similar to those of *Hispanopithecus* (Kivell and Begun 2009). The pelvis also appears to be quite flaring, as in great apes, although not elongate (Ward et al. 2008). All of this suggests an orthograde, suspensory adaptation, even though its morphology is not identical to any of the other living or fossil apes.

Conclusion

Putting the fossil evidence of locomotor evolution in hominoids together, it appears that an emphasis on deliberate arboreal quadrupedalism with weight support over multiple branches, hereafter referred to as clambering, probably served as a preadaptation for the below-branch specializations of later hominoids, as well as for *Morotopithecus*. Once the tail was lost, the tail musculature was in a position to become a strong pelvic floor, facilitating more extensive orthogrady. The strong manual and pedal grasping of multiple supports, and relatively mobile limb joints, provided a platform for more frequent hanging below branches, and this in turn would have selected for longer forearms, fingers, and toes, increased capacity for wrist adduction, and reorganization of the torso to enhance forelimb adduction. Knees and elbows would also have been selected to become even more mobile and support loading in a wider variety of postures.

All of these morphologies do not come as a thoroughly integrated package, as illustrated by *Nacholapithecus*. On the other hand, *Pierolapithecus* and perhaps *Morotopithecus* show a different suite of adaptations, with a broader rib cage and pelvis and more widely set pectoral girdle yet with a hand and foot that displays shorter phalanges. This pattern is reminiscent of that seen in extant great apes and to a lesser extent *Oreopithecus* and *Dryopithecus*. These variations underscore the growing realization that hominoids evolved below-branch arboreal adaptations more than once. Combining fossil data with data from extant apes, it seems increasingly likely that many of the postcranial and locomotor specializations of great apes may have evolved from ancestors that were more generalized, although not, perhaps, as generalized as basal hominoids like *Proconsul*.

The hypothesis that such homoplasy has possibly occurred multiple times within the Hominoidea is becoming more and more well supported by increased evidence.

All hominoids likely evolved from similar ancestors with a deliberate clambering mode of positional behavior. With similar selective pressures to exploit terminal branch arboreal settings, selection favored similar adaptations. Ateline monkeys resemble hominoids in having a slightly reduced lumbar region, broader thoracic cage, longer clavicle, mobile limb joints, and other adaptations to frequent suspension. *Epipliopithecus* also resembled lesser apes in its semisuspensory adaptations (Zapfe 1960) yet bears no close phylogenetic relation to apes.

The *Sivapithecus* dilemma initially appeared to suggest that perhaps postcranial anatomy could not be used to make phylogenetic inferences among hominoids. However, more recent discoveries of partial skeletons of *Equatorius*, *Nacholapithecus*, *Pierolapithecus*, and *Hispanopithecus*, as well as multiple postcranial elements known for *Rudapithecus*, show that, while there indeed may be postcranial homoplasy, the variation among these taxa is greater than supposed. Patterns of similarities and differences can, in fact, inform phylogenetic understanding, and so the understanding of the patterns of selection that led to the evolution of various hominoid taxa. Once paleoanthropologists can accurately interpret the phylogenetic relations among these taxa, they can reconstruct vectors of morphological change within clades. These vectors, in turn, will provide a record of the directional selection that shaped the various lineages. This provides us the opportunity to interpret the pressures that led to the observed morphological change and thus why different hominoid taxa evolved, which is what paleoanthropologists want to know above all.

The current picture of hominoid postcranial evolution is, therefore, one of recurring homoplasy. Different taxa represent different experiments in exploiting terminal branch arboreal habitats at relatively large body sizes, which requires the distribution of weight among different supports. Extant apes have all done this in somewhat different ways as did fossil ones. So rather than thinking about progressive stages evolving from an ancestral taxon like *Proconsul* to one like a modern great ape, researchers need to refocus their efforts and to explore the detailed similarities and differences among this growing collection of fossil ape skeletons to explore the diversity of locomotor adaptations within hominoids. The presence of homoplasy in hominoid evolution must not be looked at as an all-or-none phenomenon.

This approach to considering morphology is perhaps most visible to anthropologists in the origin of hominins. At present, there is no reason to assume that the most recent chimpanzee-human ancestor had such a dramatically stiffened torso, narrow cranial thorax with cranially oriented glenoid fossae and narrow scapula, or long metacarpals, and it may or may not have been a knuckle walker when terrestrial. Instead, a slightly less derived ancestor, perhaps something like *Pierolapithecus* or *Oreopithecus* in torso morphology and perhaps other characters, might be a more reasonable guess. Only more careful morphological analysis of known fossils, comparative anatomical study of extant apes, and of course discoveries of new fossils will lead to a better resolution of the ancestral condition.

Australopithecus differs from later hominins in retaining morphologies that evolved as adaptations to arboreal locomotion yet shows unequivocal strong selection for habitual terrestrial bipedality. The adaptive significance of these primitive morphologies is inherently unknowable. The extent to which *Australopithecus* and even earlier hominins, such as *Ardipithecus*, *Orrorin*, and *Sahelanthropus*, differed from the last common ancestor reveals the vector of selection that shaped hominin origins. All of these fossils indicate that the last common ancestor of them all was likely largely orthograde and adapted for some amount of vertical climbing and perhaps suspension. That *Australopithecus* evolved from a highly derived African apelike ancestor adapted to knuckle walking appears less and less likely. Rather, mounting evidence from the Miocene suggests that the australopith ancestor was orthograde, not a terrestrial quadruped (also see recent review in Crompton et al. 2008). If so, anthropologists may need to revisit the perennial question about australopith origins: the idea that hominins were selected to stand up on two legs from all fours. Rather, considering the evidence from the Miocene, including the Late Miocene hominin *Ardipithecus* (Lovejoy et al. 2009), the question that perhaps should be asked is, “why did early hominins remain orthograde when they began exploiting terrestrial niches?”

To understand why our own lineage diverged from that of other apes, it is necessary first to understand the ancestral morphology from which hominins evolved. Only then can paleoanthropologists determine, for example, whether australopith forearms reduced from the primitive condition or not. The expanding hominoid fossil record affords us ever more opportunities to appreciate the diversity, past and present. What may seem at first like an increasingly confusing picture of homoplasy must be viewed as an opportunity to obtain a more accurate and nuanced understanding of the adaptive diversity present throughout the hominoid radiation.

Cross-References

- ▶ Defining Hominidae
- ▶ Dental Adaptations of African Apes
- ▶ General Principles of Evolutionary Morphology
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Origin of Bipedal Locomotion
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ The Species and Diversity of Australopiths

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Hominoid Cranial Diversity and Adaptation

Alan Bilsborough and Todd C. Rae

Contents

A. Bilsborough (✉)
Department of Anthropology, University of Durham, Durham, UK
e-mail: alan.bilsborough@durham.ac.uk

T.C. Rae
Department of Life Sciences, University of Roehampton, London, UK
e-mail: t.rae@roehampton.ac.uk

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Abstract

The hominoid cranium represents a tightly constrained, functionally and developmentally integrated structure subject to multiple selective influences. Modern apes are the remnant of a much more diverse radiation, raising issues about their suitability as models for earlier hominoids. Among gibbons the folivorous siamang is cranially distinctive. The markedly airorynchous *Pongo* is cranially highly variable and lacks the anterior digastric muscle, thereby contrasting with other hominoids (except *Khoratpithecus*). African apes share a common cranial pattern differentiated by varying growth rates, not duration. Airorhynchy is common among fossil hominoids and differentiates hominoids from non-hominoids, suggesting that African ape klinorhynchy is derived. Bonobos are cranially smaller, lighter, and less dimorphic than chimpanzees. These are comparatively uniform, with extensive overlap between subspecies, whereas gorillas display considerable contrasts, especially between east and west populations. Early Miocene hominoids are already cranially diverse, with most species probably soft- or hard-fruit feeders. Middle and Late Miocene forms from Africa, Europe, and Western Asia are thicker enameled with more strongly constructed crania suggesting harder diets, although *Dryopithecus* (soft frugivory) and *Oreopithecus* (folivory) are exceptions. South and East Asian fossil hominoid diets ranged from soft fruits through harder items to bulky, fibrous vegetation. All extant ape crania are relatively lightly constructed compared with fossil forms, again prompting questions about their suitability as adaptive models of earlier hominoids.

Introduction

The hominoid fossil record has expanded markedly over the last two decades, sufficiently to indicate marked morphological diversity. This in turn reflects a major radiation or, more likely, series of radiations. The great bulk of the material is from Miocene contexts – apart from hominins there is still comparatively little from Plio-Pleistocene deposits – so that fossil and living hominoids are largely detached from one another. Whatever the details of this array, it is clear that the extant nonhuman apes represent but the surviving fragment of a significantly more numerous, geographically more extensive, and ecologically more diverse group of catarrhine primates. The extremely restricted modern comparative base and its (at best) tenuous links with the earlier material pose real challenges for adaptive and phylogenetic interpretations of the fossil hominoid record.

An outcome of this is that detailed phylogenies often differ appreciably from author to author, depending on the significance accorded to particular apomorphies and on the extent to which other similarities are deemed homoplasies. The upshot is a whole series of individual phylogenies and widespread disagreement about the status of particular groups which usually translate through into the taxonomies preferred by individual researchers. Since the thrust of this chapter is primarily adaptational, we do not concern ourselves with taxonomic or phylogenetic details; in what follows suprageneric categories are used informally and generally follow majority consensus usage. For those requiring more detailed information on phylogenetic issues concerning the Miocene hominoid record, the chapters "▶ Fossil Record of Miocene Hominoids" and "▶ Postcranial and Locomotor Adaptations of Hominoids," Vol. 2, and the papers by Harrison (2002), and contributors in Hartwig (2002) are excellent recent surveys.

Cranial form is influenced by multiple factors. Functionally, the head houses the visual, olfactory, and auditory organs and those of vocalization, taste, and balance; it contains the openings for the respiratory and alimentary tracts; and it houses and protects the brain. It incorporates structures for food acquisition and processing, while postural and respiratory factors influence basicranial morphology. Its superficial tissues may be patterned and convey information to conspecifics about sex and ontogenetic status. The interplay of these features, and especially the size and configuration of those concerned with food processing relative to neurocranial proportions, may lead to the development of external structures such as crests and tori on the skull. There are clearly intense selection pressures determining effective developmental and functional integration of these varied aspects of cranial function throughout the individual life cycle.

Fleagle et al. (2010) undertook a 3D geometric morphometric study (Procrustes and Principal Components Analysis) of primate crania to quantify broad aspects of cranial diversity. Their first PC differentiated on cranial flexion, orbit size and orientation, and relative brain size, while PC 2 reflected differences in cranial height and snout length. *Eulemur*, *Mandrillus*, *Pongo*, and *Homo* represent the limits in cranial shape. Overall, hominoids display the greatest diversity in cranial shape among extant primate clades, although much of this is driven by the atypical and highly distinctive cranium of *H. sapiens*.

Adult African apes including humans, known as hominids, share a broadly common pattern of covariation in cranial traits, with the oral and zygomatic regions primary integrative influences and with a lesser contribution from the nasal region, i.e., those craniofacial components primarily associated with mastication (Ackermann 2002, 2005). This differs from the pattern in both Old and New World monkeys, in which the oral region is the exclusive primary contributor to facial integration. Ackermann suggests that this contrast may reflect innovatory functional or developmental shifts after the differentiation of hominoids from other Anthropoidea or be an allometric consequence of increased body size. Orangutans and gibbons were not represented in the analyses, but the extent to which they share the primary oral/zygomatic integrative pattern should help decide between these possibilities and assist in determining whether the pattern is a hominoid or hominid synapomorphy.

There are similar allometric patterns in the midface and common opposite relationships between lower and upper face in the adults. Whereas visual inspection and morphological distance place adult *Pan troglodytes* and *Gorilla gorilla* close together and *Homo sapiens* distant, craniofacial covariation patterns accord with molecular data in indicating closer affinity between *P. troglodytes* and *H. sapiens*, with *G. gorilla* distant (Ackermann 2002). Such concordance, however, does not hold throughout ontogeny, with differing patterns of affinity between juveniles and subadults of the above taxa on the one hand and infants and “adolescents” on the other (Ackermann 2005).

Nonetheless, some general patterns emerge: in particular, across the species earlier and later (subadult and adult) integration appears to reflect different drivers. Oral integration is especially influential in the earlier stages, as well as thereafter, but there are specific differences in the onset of zygomatic integration. In *P. paniscus* and *P. troglodytes*, it appears during the juvenile/adolescent periods, whereas in *Gorilla* it occurs from infancy, perhaps a correlate of its rapid growth. In all species, zygomatic integration intensifies in later ontogeny. Where evident, nasal integration occurs in mid-/late ontogeny, its intensity varying inversely with oral integration, suggesting that separate developmental modularities underlie these regions. While the most highly integrated species as adults, humans are more developmentally labile than the other African apes prior to maturity. While differing in detail, however, all species show a common pattern of intensified integration throughout development, with a particular shift toward more constrained variation around sexual maturity or just after. The extent to which these similarities reflect shared, genetically determined, developmental pathways, or common selection pressures associated with vital functional requirements – the need for effective food processing mechanisms, for instance – remains to be determined. In the latter case, some proportion of the resemblance could be homoplastic.

A recent study by Singh et al. (2012) based on covariation in 56 morphometric landmarks representing the functional modules of the face, vault, and basicranium (Moss and Young 1960; Moss 1973) extends the analysis of cranial integration to include *Pongo* as well as the African apes. The results point to complex integrated shape changes, but despite marked contrasts in adult cranial morphology, all species display close similarities in covariation patterns between the face, basicranium, and vault. The implication is that the pattern of hominoid cranial integration has been conserved at least since the separation of the Asian ape and hominid clades, presumably due to strong stabilizing selection constraining developmental processes.

While some cranial features are relatively invariant in catarrhines (e.g., positioning of orbits; structure of the auditory region), others (e.g., orbital size and shape) are highly variable within genera, species, and even subspecies (Seiffert and Kappelman 2001). Some features seem to be determined less by their "primary" function than by influences reflecting the interactions of other functional systems; e.g., the size and proportions of the orbits appear to be determined more by the growth trajectories of the mid- and upper face and by requirements to resist the biomechanical forces generated by food processing as they affect those regions than by the dimensions of the visual organs housed within them (Schultz 1940). Other traits (e.g., the structure of the nasal floor and premaxilla/palatal relationships; Ward and Kimbel 1983; Ward and Pilbeam 1983) exhibit contrasts, the functional basis of which is poorly understood, but which serve as useful phylogenetic indicators (see below).

The compilation of long lists of character states as the raw data for computer-based cladistic analyses has been criticized by some (Rak 1983; Suwa et al. 1997; Asfaw et al. 1999, 2002) as resulting in the fragmentation or "atomization" of morphology as multiple discrete traits, rather than an integrated whole. It is therefore worth noting here the recent accounts that stress the importance of broader functional and developmental perspectives in analyzing morphology and its evolutionary/phylogenetic and adaptive contexts (Lovejoy et al. 1999, 2003; Lieberman et al. 2000a, b; McCollum and Sharpe 2001; Rae and Koppe 2000; Ackermann 2002, 2005; Singh et al. 2012). These build upon earlier studies such as those of Moss and Young (1960), Moss (1973), Enlow (1968, 1990), and Cheverud (1982, 1996); and biomechanical analyses such as that of Endo (1966); see also Rak (1983).

An example of this approach is McCollum's analysis of *Paranthropus* cranial morphology (McCollum 1997, 1999; McCollum and Sharpe 2001), which concludes that limited changes in the relative growth rates of jaws and teeth on the one hand and of the orbit and upper face on the other would be sufficient to produce in mature individuals the distinctive set of features that characterize the robust australopithecine cranium/face. Such growth rate changes are doubtless under simple, limited genetic control and, as such, are readily elicited in appropriate selective contexts. It is not difficult to envisage comparable pressures operating on Miocene hominoids, and so a variety of cranial forms thereby rapidly resulting from relatively limited genetic changes. So, for example, the contrasting morphologies of *Proconsul* and *Afropithecus* might both be derived relatively simply from an Oligocene precursor such as *Aegyptopithecus*, and purely phenetic measures of affinity between these forms could be seriously awry as indicators of phylogenetic relationship.

One outcome of cladistic studies has been the general recognition of the pervasiveness of homoplasy in the fossil record. From an adaptive perspective, instances of homoplasy can provide important clues as to the contexts of, and likely selective forces impacting on, hominoid communities. In such cases, the influence of phylogenetic constraint and contingency may be considerable. Minor initial differences between spatially distributed populations of a single species (or of closely related species), when further influenced by bottlenecking or other stochastic factors – easily occurring in small, localized arboreal groups, where gaps in tree cover impede gene flow – may result in significantly different morphological outcomes as responses to common selection pressures associated with similar niches. The evolution from the nasal/palatal structure seen in *Proconsul* and other Early Miocene forms of distinct anatomical configurations for that region in Middle/Late Miocene Afro-European and Asian hominoids may be an example of such a process and its outcomes.

A fundamental division of extant hominoids is that between gibbons (hylobatids) and large-bodied apes – the Asian orangutan (*Pongo*) and the African chimpanzee and bonobo (*Pan*), gorilla (*Gorilla*), and human (*Homo*), although the last taxon will be discussed elsewhere. *Pongo* and *Pan* are both largely frugivorous, with common dental adaptations (large anterior teeth and relatively small check teeth with enamel wrinkling) but differing in cranial features, whereas the more herbivorous *Gorilla* closely resembles *Pan* cranially despite its contrasting dietary niche (see below). These differing patterns of affinity illustrate the importance of developmental constraints and phylogenetic inertia in determining morphology and thus the lack of any necessary one-to-one correspondence between morphology and adaptation (for further discussion of this, see below).

It is possible in principle to extend the limited insights provided by the few extant great apes into the earlier radiation by supplementing them with modeling based on early hominins, which can be thought of as phenetically and adaptively "apes" in some respects. Apart from the dangers of circular reasoning (using modern ape data as inputs into constructing early hominin models that are then used to "extend" the ape comparator base) and the appropriateness of such models (what form and degree of terrestrial orthogrady, if any, is compatible with using hominins as analogues for non-hominins?), however, there are major issues of contextual relevance.

All extant apes (here and throughout meaning non-hominin hominoids) and early hominins are essentially from tropical contexts (forest, woodland, and savannah) with none present in higher latitudes, reflecting a comparatively narrow environmental range compared with earlier ape habitats. Even incorporating early hominins within the comparator base provides a time depth of little more than 4+ Myr, characterized by broadly modern faunas that include groups rare or absent in the earlier record. In contrast, Miocene hominoids are components of markedly distinct and diverse faunas, often including entire mammalian families now extinct. So community relationships within earlier faunas will have differed from contemporary ecological webs, and the place(s) of earlier hominoids in their ecological communities are unlikely to correspond closely to those of modern ape analogues.

An obvious primate example of this is the expansion and radiation of cercopithecoids over the last 10 Myr or thereabouts, so forming a major dimension of the community ecology of all recent hominoids, unlike that of earlier taxa. Floral communities also fluctuated as climatic conditions changed, with notable contrasts between Early to Middle Miocene habitats and those of the Late Miocene and Pliocene.

Against these differentiating features are some factors that make for modeling continuity: the range of potential (plant) food items is limited, and their physical properties even more so, limiting the nature and magnitude of the masticatory forces influencing hominoid cranial morphology. Metabolic and biomechanical constraints on body size and on locomotor form and activity, allometric influences on growth, and the functional and developmental interdependences of cranial form noted above all allow for a more comparative approach to hominid cranial variation. Below we review the probable ancestral condition for Hominoidea, then examine some aspects of cranial form in extant nonhuman hominoids before summarizing craniodental information on the more complete fossil forms.

Ancestral Hominoid Cranial Morphology

The combination of outgroup analysis of extant forms and the morphology of stem catarrhines provides an indication of the ancestral hominoid cranial morphotype. The Fayum fossil primates represent an early diversification of basal catarrhines, presumably reflecting dietary specialization. For example, the small and dentally and gnathically primitive *Catopithecus* (35.5–36 Ma) combines the characteristic 2.1.2.3 dental formula, postorbital closure (primarily formed from the zygomatic), fused frontals, and C^1/P_3 honing facet with triangular upper molars with only limited hypocone development and lower molars with high trigonids and sharp crests. *Catopithecus* had a deep and projecting face, with an especially broad premaxilla; small, widely separated orbits; and a small neurocranium with anteriorly prominent temporal lines merging to form a sagittal crest along the rear half of the vault and well-developed nuchal crests. The tympanic region is like that of platyrrhines, not catarrhines, and the mandibular symphysis is unfused. The anterior dentition displays broad, spatulate incisors and projecting, dimorphic canines, suggesting a predominantly frugivorous niche.

Many of these features, including the contribution of the premaxilla to facial proportions, small neurocranium with marked muscle attachments and pronounced ectocranial cresting, and ceboid-like tympanic region, are also seen in the younger (33.1–33.4 Mya) and dentally more derived propliopithecid *Aegyptopithecus*. The zygomatic is again deep and the face in general strongly constructed, with a characteristic angled profile, and the mandibular symphysis is fused. The gonial region is strongly constructed and the ramus broad and high. The interorbital distance is again broad, with bony septa separating the high, narrow orbits and the interorbital region projects anteriorly from the medial orbital margins. Semicircular supraorbital tori extend over each orbit and, meeting medially, anteriorly bound a diamond-shaped frontal planum, whose posterior limits are defined by the anterior temporal lines. The anterior teeth are small compared to the postcanine dentition, making a narrow anterior palate. The molars are inflated and highly bunodont, especially the second, and the elongated lower third molar has a centrally placed hypoconulid; the trigonid is reduced in occlusal area and height and lacks the paraconid, while the talonid is expanded with a large distal fovea. The upper molars are quadritubercular, with a well-developed hypocone. There is marked canine dimorphism, with upper canine honing capabilities increased by a lengthening of the anterior surface of P_3. Overall morphology points to the generation of greater occlusal pressures than in *Catopithecus* and a craniofacial form better able to withstand the resulting forces.

When the details of stem catarrhine facial morphology are considered with the evidence from extant outgroups of the Catarrhini (e.g., Platyrrhini), it is possible to infer the major changes that underlie the ancestral hominoid craniofacial skeleton. Unlike stem catarrhines or platyrrhines, hominoids are characterized by a palate that is wide at the level of the canines, nasals that are nonprojecting and lie near the medial orbital margin in transverse section, and a premaxillomaxillary suture that contacts the nasals inferiorly near the nasal aperture (Rae 1999). Unlike previous interpretations, it is also evident that the overall shape of the ancestral hominoid morphotype is more cercopithecine-like (Benefit and McCrossin 1991), with tall zygoma and a deep face. This suggests that the shared craniofacial configuration of gibbons and colobine monkeys (short face, sloping zygoma) is convergent.

Extant Hominoids

Hylobates

Gibbons represent a radiation of small-bodied, brachiating suspensory hominoid species with attendant postcranial specializations, distinguished from each other primarily by pelage color and patterning and by vocalization. Four main groups are usually recognized, sometimes accorded subgeneric or generic rank, depending on the author. Three groups – *Hylobates hoolock*, *H. concolor*, and *H. syndactylus* – are comparatively well defined; the *H. lar* group is more problematic. Valuable reviews of extant gibbon characteristics and diversity include Groves (1972), Marshall and Sugardjito (1986), and Groves (2001); see also Geissmann (2002) and Mootnick and Groves (2005) for recent findings on gibbon diversity that support generic distinction, although the traditional use of the single genus *Hylobates* is maintained here.

Gibbons are craniodentally primitive in some characteristics (see above), compared with other extant hominoids, whether by plesiomorphy (McNulty 2004) or reversal (Rae 2004); appreciation of this led to the realization that similarities with Miocene taxa, such as *Limnopithecus* and *Pliopithecus*, previously taken as grounds for regarding these as likely gibbon ancestors, do not betoken any especially close phylogenetic relationship. The upshot is that, in the absence of a fossil record other

Fig. 1 (*Upper*) Frontal and profile views of *H. hoolock* skull (Photograph © The Grant Museum of Zoology, University College London). (*Lower*) Frontal and profile views of *H. symphylangus* skull (Photograph courtesy C.P. Groves)

than dental remains from Quaternary deposits of China and Indonesia referable to the modern genus, the early evolutionary history of gibbons is wholly obscure.

Overall, the *Hylobates* skull is rather lightly constructed (Fig. 1). The neurocranium is thin walled and the vault low and ovoid in profile, with a capacity of about 80–125 cm^3. The frontal extends rearward between the parietals, and in most individuals the sphenoid sutures with the parietal on the vault wall. The orbits are rectangular and relatively large, with strongly developed lateral margins; a torus also develops laterally above the orbits but is not continuous, fading out medially. The lacrimal fossa extends beyond the orbital rim onto the maxilla, and the interorbital breadth is large; the short, broad nasals are usually fused above the ovoid nasal aperture. Overall the face is short, broad, and fairly projecting. Within the nasal cavity, the premaxilla and maxillary palatine process are separated by broad palatine fenestra linking the nasal and oral cavities (Fig. 2 upper left); the vomer extends only as far as the fenestra, and the bony nasal septum is continued anteriorly by the premaxillary prevomer, which fuses to the vomer and forms a small bony crest in the incisive region in all gibbon species except the smallest, *H. klossi* (McCollum and Ward 1997). The palate and mandible are long; both corpus and symphysis are comparatively lightly built, although external thickening of the latter may be evident in some individuals, as well as the usual internal reinforcement by a superior transverse torus. The ramus is short, broad, and vertical, with some expansion of the gonial region.

Reflecting gibbons' predominantly frugivorous niche, the anterior dental arcade is relatively broad compared with the rear. The upper incisors are markedly heterodont – I^1 broad and spatulate and I^2 narrow and pointed – the lowers more similar, vertically implanted, and subequal in size. The canines are long, curving, transversely slightly narrowed, and sharply pointed, with minimal sexual

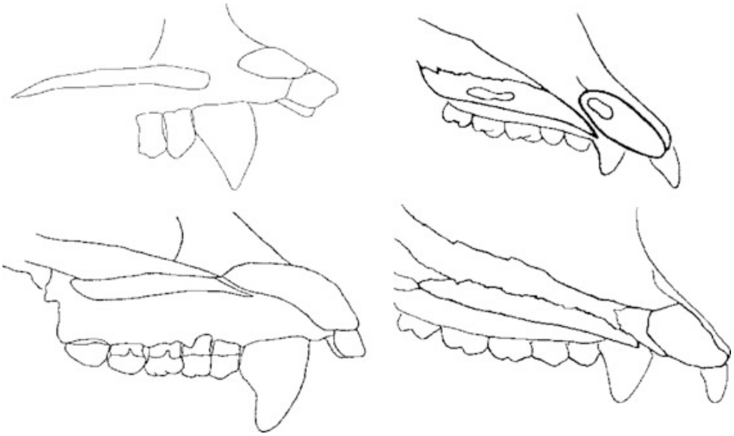

Fig. 2 Subnasal morphology of hominoids seen in sagittal section. *Upper left*: *Morotopithecus*, showing no overlap of the premaxilla on the maxilla (the primitive condition seen in extant *Hylobates* and most fossil hominoids). *Lower left*: *Pongo*, showing the smooth overlapped subnasal condition also seen in *Sivapithecus*. *Right*: *Pan* (*upper*) and *Gorilla* (*lower*) showing the stepped overlapped condition usual in extant African apes (Modified after Ward and Kimbel (1983))

dimorphism. There is well-developed honing of the upper canine against the long, highly compressed anterior face of the sectorial P_3, which is orientated in line with the molars. Cheek teeth exhibit considerable metric and morphological variation, but the rear molars are usually reduced compared with the first and especially the second molars except in *H.* (*Symphalangus*) *syndactylus* (see below).

The basicranium is long, with the foramen magnum and occipital condyles well behind the auditory meatus; there is no distinct mastoid process. The nuchal area is quite extensive, rising well up the occipital, with a distinct crest laterally that usually fades medially, although it may be continuous in some individuals. A sagittal crest is usually absent but may occur in small-brained individuals.

Detailed accounts of intra- and interspecific variation in *Hylobates* are given in Groves (1972, 2001) and Marshall and Sugardjito (1986) as above. Albrecht and Miller (1993) summarize their reanalysis, with caveats, of Creel and Preuschoft's (1976) craniometric data: canonical variate analysis (CVA) reveals *H. hoolock*, *H. concolor*, and *H. syndactylus* as cranially distinct from each other and from the *H. lar* group. This consists of a primary cluster including *H. lar*, *H. agilis*, *H. moloch*, and *H. muelleri* subspecies, with *H. pileatus* as an outlier and *H. l. vestitus* and *H. klossi* grouped together as a second, distinct, outlier. A subsequent analysis (Creel and Preuschoft 1984) produced patterns of resemblance that generally accord with geographical distribution but not always with the usually recognized species limits. A recent study by Leslie (2010) extends analysis to the relative orientation of internal cranial features and their variation across the recognized hylobatid groupings; the findings generally accord with those of the earlier studies based on external cranial features.

Fig. 3 Frontal and profile views of *Pongo pygmaeus* skull (Specimen courtesy of the Oxford University Museum of Natural History)

The only distinctive form noted here is the siamang *H.* (*S.*) *syndactylus* (Fig. 1, lower). This large, heavily built gibbon is more folivorous than other taxa and has a larger cranial capacity, a long, broad palate, and an inflatable air sac in the throat to aid calling. Postorbital constriction is more marked, and, despite the larger cranial capacity, sagittal cresting is both more frequent and larger than in other gibbons, an allometric correlate of greater body size (see below).

In the dentition, the canines are less lingually curved than in other gibbons, the protocone on P^3 and P^4 larger; and on the upper molars, crowns are elongated, the hypocone variable in size, and lingual cingula almost always absent. Third molar reduction occurs in only a minority of cases, and some individuals possess supernumerary molars. Again consistent with its more folivorous niche, relative shearing-crest development is greater than in other gibbon species (Kay and Ungar 1997, 2000). *H.* (*S.*) *syndactylus* has a larger, more airorhynchous (i.e., more dorsally flexed) face than other gibbons (Shea 1988) – see below.

Pongo

The Asian great ape, the orangutan, exhibits a distinctive overall cranial form (Fig. 3). In profile the large face is markedly prognathic subnasally, with a projecting, convex alveolar clivus. The comparatively small neurocranium is set above the facial skeleton, so that both frontal and occipital contours are relatively vertical. The orbits are elliptical, with their major axis vertical, and are surmounted by separate semicircular supraorbital costae rather than a continuous torus. The interorbital distance is very small, the ethmoid correspondingly constricted and set at a lower level than in the African apes (Shea 1988). There is no frontoethmoid sinus (Fig. 4), and the floor of the anterior cranial fossa forms a large part of the orbital roof (Winkler et al. 1988). In the fossa, the two wings of the frontal bone fail to meet behind the ethmoid, which retains contact with the sphenoid. The nasal bones are small, typically fused at an early age, and continue beyond the frontomaxillary suture, extending as a narrow wedge into the glabellar region of the frontal. On the medial orbital wall the lacrimal sutures with the ethmoid.

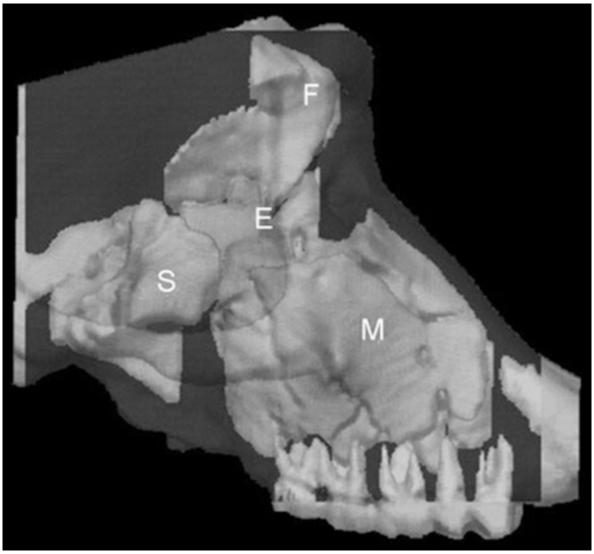

Fig. 4 Virtual three-dimensional reconstruction of *Pan* cranium from serial CT scans. The bone has been made transparent to show the paranasal sinuses and tooth roots. *F* frontal sinus, *E* ethmoidal sinus, *S* sphenoidal sinus, *M* maxillary sinus (Image courtesy of T. Koppe)

The midface region is short, the zygomatics are wide, deep, and flared, and there is usually a pronounced notch on the zygomatic process of the maxilla. The nasal cavity is tall and broad, the maxillary sinuses invade the interorbital pillar (sometimes as far superior as the frontal), and the lateral maxillary walls are obliquely inclined. The convex nasoalveolar clivus passes smoothly into the nasal cavity, extensively overlapping the anteriorly thin maxillary palatine process without a stepped incisive fossa; the fossa and canal are narrow, the latter long and orientated almost horizontally (Fig. 2 lower left). The vomer usually extends to the rear of the incisive canal but occasionally does not, in which case a small prevomer may be present (Ward and Kimbel 1983; Ward and Pilbeam 1983; McCollum and Ward 1997). Overall the palate is orientated anterosuperiorly.

The mandible is massive, the symphysis reinforced by a robust superior transverse torus and an especially pronounced inferior transverse torus extending back as far as P_4 or M_1 (Brown 1997). The corpus is deep and comparatively short. As in the African apes, there is a strongly developed platysma muscle extending laterally over much of the facial musculature and strongly attached to the swollen base of the mandibular corpus from the symphysis to the area of masseter insertion. Brown and Ward (1988) speculate that the massive platysma is associated with the orangutan's extensive laryngeal air sac system – greater than in other apes – aiding the regulation of air pressure and volume within the sac during vocalization. A distinctive feature of *Pongo* is the absence of the anterior digastric muscle (and so of the digastric fossae on the base of the symphysis) and associated separation of the posterior digastric from the hyoid and stylohyoid muscle (Dean 1984; Brown and Ward 1988). Instead the large posterior digastric, originating on the cranial base adjacent to *rectus capitis lateralis*, inserts onto the gonial region between the medial pterygoid and masseter muscles, acting to depress the mandible.

The orangutan's mylohyoid muscle is especially well developed, as are the geniohyoids. *Rectus capitis lateralis*, originating from a narrow area on the front of the atlas and inserting on the basioccipital anterior to the foramen magnum, is a more fan-shaped muscle than its homologue in the chimpanzee.

The cranial base is wider than in the African apes (Dean and Wood 1981, 1984), but the eustachian process is much smaller, providing the origin for only *tensor palati*, with *levator palati* originating from the apex of the petrous temporal (Dean 1985). The mastoid processes are poorly developed. In the articular region, there is a long preglenoid plane, an indistinct articular eminence, and a prominent postglenoid tubercle. The roof of the glenoid fossa is coronally oblique, slightly sloping inferomedially, so that the entoglenoid is less prominent than in the African apes. The temporomandibular ligament is well developed laterally but lacking the deeper horizontal band, suggesting closer approximation of the rear of the working condyle and the postglenoid tubercle during chewing (Aiello and Dean 1990).

The foramen magnum and occipital condyles are set well back on the skull base. A nuchal crest is present in all mature individuals, and a prominent sagittal crest develops posteriorly in most males, uniting with the nuchal crest but, reflecting the orangutan's greater airorhynchy, typically not extending as far beyond the rear of the vault proper as in *Gorilla* (see below). Anteriorly the temporal muscles diverge as lines or simple crests bounding a triangular area of the frontal. As in the African apes, the bulk of the *temporalis* muscle is orientated obliquely, with an emphasis on the posterior fibers.

The dentition reflects the orangutan's predominantly frugivorous niche. The upper incisors are the most heteromorphic of any extant hominoid: I^1 is very broad and spatulate, but I^2 is smaller, more pointed, and more convex in curvature. Well-developed median and marginal ridges reinforce the incisor crowns in biting. Lower incisors, high crowned and narrower than the uppers, are also reinforced by lingual ridging. Canines are conical, markedly dimorphic, and especially robust in males; females display more pronounced lingual cingula. Upper premolars are bicuspid; P_3 is sectorial with a narrow, elongate protoconid as the honing face; P_4 is bicuspid. Upper molars are more oval in occlusal outline than in other apes (Swarts 1988; Swindler and Olshan 1988; Uchida 1998b). Cheek teeth are relatively large compared to body size, low crowned, and with extensive, deep secondary wrinkling that further increases occlusal area. Molar shearing crests are rather well developed considering the emphasis on fruit (although significant quantities of bark and leaves are also ingested), exceeding those of chimpanzee species but considerably less than gorillas (Kay and Ungar 1997). They perhaps provide an instance of phylogenetic inertia, suggesting a more folivorous ancestor.

Orangutans are remarkably variable in cranial morphology (Wood Jones 1929; Röhrer-Ertl 1988a, b; Winkler 1988). Röhrer-Ertl (1988b) has shown that the most stable region is the midface, other cranial areas varying according to age, sex, dental eruption and masticatory development, hormonal status, dietary composition, and tooth use. Both the neurocranium and face exhibit greater growth in breadth than in length or height, a differential that is more marked in males than in females. While there is much individual and intrapopulational diversity, at least some variation reflects geographic factors: Groves (1971, 1986, 2001) and

Röhrer-Ertl (1988a, b) review cranial patterning and Brown (1997) mandibular form, while Uchida (1998b) summarizes dental differences. Within a context of admittedly high variability, Sumatran orangutans are characterized by an oblique but straight (not concave) facial profile with highly protuberant anterior teeth, a convex cheek region lacking a suborbital fossa, relatively short nasals, a shorter neurocranium but with a longer nuchal region, and a longer foramen magnum. The mandibular symphysis tends to be long and narrow, with an extensive inferior transverse torus. Dentally they exhibit relatively small paracones on P^3 and M^1 compared with their Bornean counterparts, M^1 larger than M^2 rather than subequal, and a broader M_3.

Bornean orangutans have a generally more prognathous and concave facial profile, display a distinct suborbital fossa on the cheek, and have more labially positioned incisors, a “trumpet-shaped” nasal aperture that becomes triangular in cross section at the level of the nasal tubercle (Röhrer-Ertl 1988a), and a more prominent interorbital pillar (Groves 2001). Their mandibles are deeper and broader anteriorly, and the symphysis is usually larger, thicker, and more bulbous than that of Sumatran orangutans. Taylor (2006) explored the relationships between feeding behavior, diet, and mandible morphology, specifically the greater exploitation of bark and relatively tough vegetation during low fruit periods by some Bornean orangutan populations compared with Sumatran ones. She found that the Bornean mandibles display a relatively deeper corpus, deeper and wider symphysis, and relatively greater condylar area, arguing that these features enable greater load resistance to masticatory and incisal forces, reflecting ingestion of harder food items. There is a gradient within Borneo, with populations in NE Kalimantan and Sabah *(P. p. morio)* displaying fullest expression of these traits, those in SW Kalimantan *(P. p. wurmbii)* rather less, and with those in NW Kalimantan (*P. p. pygmaeus*) generally intermediate between *P. p. morio* and the Sumatran mandibles, thus implying a spectrum of hard food exploitation in Bornean orangutans.

There is other craniodental differentiation within Borneo between populations from Sabah, NW and SW Kalimantan separated by the Kapuas River (Groves 1986, 2001; Courtney et al. 1988; Groves et al. 1992), often of comparable magnitude to that between Bornean and Sumatran orangutans. For example, Taylor and Schaik (2007) document variability in absolute and relative brain size in orangutan populations, finding significantly smaller brains among the north east Kalimantan/Sabah group (*P. p. morio*) compared with those from elsewhere in Borneo and from Sumatra. They relate these findings to differences in resource quality and life history: *P. p. morio* has the least productive habitat, lowest energy intake during extended periods of scarcity, and the shortest interbirth intervals, arguing that brain size and prolonged food scarcity may be inversely correlated. Uchida (1998b) was unable to identify any consistent pattern of dental differences between *Pongo* populations from W Borneo, SW Borneo, and Sumatra, with the Bornean groups often as distinct from each other as either was from the Sumatran sample. Bornean orangutans were significantly different from each other (but not from Sumatra) in P_4 and M_1 shape, but virtually identical in their narrow M_3 shape, with Sumatran orangutans having broader rear molars. Differences in molar cusp proportions showed similarly inconsistent patterning between the three groups. There were no obvious links to dietary differences, and Uchida concluded that on dental evidence, river and mountain systems within Borneo were as significant biogeographic barriers and so promoters of differentiation, as flooding of the Sunda shelf.

Bornean and Sumatran orangutans have generally been accorded subspecific status as *Pongo pygmaeus pygmaeus* and *P. p. abelii*, respectively (Schwartz 1988). In his latest revision, however, Groves (2001) distinguishes them as separate species (*P. pygmaeus* and *P. abelii*) on the basis of the more comprehensive morphological information now available and molecular differences well above levels usually associated with subspecies, which indicate a long period (c. 1.5 Ma) of isolation between the two forms. He also formalizes the intra-Bornean diversity noted above as subspecies of *P. pygmaeus*. This taxonomic framework, which is also followed, for example, by Taylor (2006), is reinforced by a study of multiple genetic loci which extends Sumatran and Bornean orangutan divergence back to 2.7–5.0 Mya, with isolation thereafter (Steiper 2006). The data also point to contrasting population histories, with Bornean orangutans having undergone recent population expansion beginning 39–64 Kya, while Sumatran populations remained stable.

The Sumatran and Bornean orangutans also exhibit developmental contrasts. Uniquely, male Sumatran orangutans may delay for many years full expression of secondary sexual characters, including their characteristic cheek flanges, whereas such long delays are much less common among Bornean males. Pradhan et al. (2012) relate such flexible developmental arrest to sociobiological factors and in particular to the potential for high-ranking males (flanged or unflanged) to monopolize sexual access to females. When the potential is low, no developmental arrest is the prevailing pattern, whereas at high monopolization potential the flexible, arrested development pattern is the stable one. Their model accords with field data indicating different monopolization potentials between Bornean and Sumatran flanged males and a lower proportion of these in the Sumatran orangutan population. Harrison and Chivers (2007) relate the evolution of developmental arrest to the onset of longer, more severe periods of low food availability reflecting climate change 3–5 Mya, with females dispersing more widely in search of food and adult flanged males less able to effectively guard a female harem, so providing an opening for the unflanged male as a quiet, quick, opportunistic "sexual predator."

Hominoids exhibit more dorsal flexing of the face relative to the cranial base (airorhynchy) than non-hominoids; their orbital axes and palates are both shifted more dorsally relative to their degree of basicranial flexion than those of other primates (Ross and Ravosa 1993; Ross and Henneberg 1995). While the functional basis for this is disputed (Ross and Ravosa 1993) and may well have multiple causes, within this context many of the orangutan's distinctive features can be plausibly related to its extreme airorhynchy (Delattre and Fenart 1956, 1960; Biegert 1964; Shea 1985, 1988; Brown and Ward 1988). Biegert (1964) argued that the hypertrophied laryngeal sac in *Pongo* is a prime determinant of its skull form, comparing it with the enlarged hyoid and associated throat organs of *Alouatta*. Shea (1985, 1988) and Brown and Ward (1988) have criticized this interpretation. Shea considers laryngeal specialization as just one potential determinant of airorhynchy, interacting with other factors, largely unknown. Brown and

Ward consider the *Pongo-Alouatta* analogy invalid in view of contrasts in the submandibular anatomy of these two genera, and it has also been rejected by Hershkovitz (1970) and Zingeser (1973).

Shea argues that pronounced dorsal flexion of the face links *Sivapithecus* and *Pongo* and that a degree of airorhynchy (although not to the extent seen in these two genera) is primitive for catarrhines and hominoids generally. On this view, the more ventral positioning of the face relative to the neurocranium seen in African apes and hominids is synapomorphous and, as such, a significant phylogenetic indicator (see also Ross and Ravosa 1993; Ross and Henneberg 1995; and below). The distinctiveness of *Pongo* is emphasized by its pattern of ectocranial suture closure (Cray et al. 2010). Vault suture synostosis is similar to *Gorilla* (but contrasts with that of *Pan* and *Homo* – see below), but the lateral-anterior pattern of fusion, with its strong superior to inferior gradient, is unique to *Pongo*, reflecting its relative phylogenetic isolation among hominoids.

The African Apes

As is well known, the African apes (hereinafter meaning gorillas, chimpanzees, and bonobos, i.e., non-hominin hominines) share a basic similarity of cranial form and in many respects are scaled variants of a common bauplan (Figs. 5 and 6). Many of the craniodental differences between them have been related, with varying degrees of success, to differences in dietary niche (see Chaps. "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1, "▶ Geological Background of

Fig. 5 (*Upper*) Frontal and profile views of *Pan paniscus* skull (Specimen courtesy of the Oxford University Museum of Natural History). (*Lower*) Frontal and profile views of *Pan troglodytes* skull (Specimen courtesy of the Oxford University Museum of Natural History)

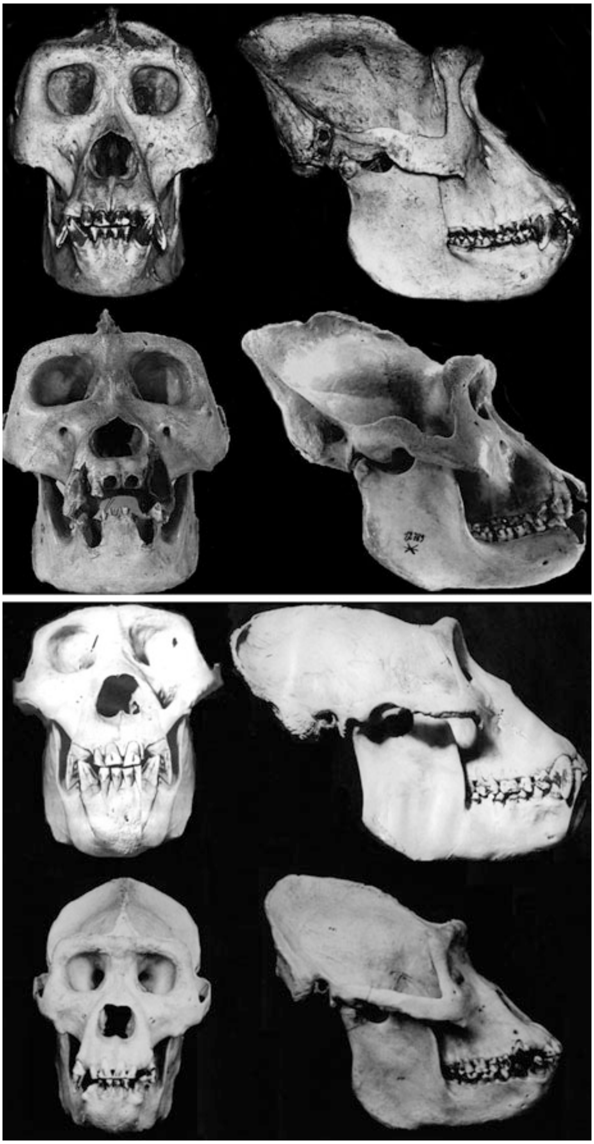

Fig. 6 *Top* (*Upper*) Frontal and profile views of *Gorilla gorilla gorilla* skull (Photograph courtesy of C.P. Groves). (*Lower*) Frontal and profile views of *G. g. diehli* skull (Photograph courtesy of E. Sarmiento). *Bottom* (*Upper*) Frontal and profile views of *G. g. graueri* skull (Photograph courtesy of C.P. Groves). (*Lower*) Frontal and profile views of *G. g. beringei* skull (Photograph courtesy of C.P. Groves)

Early Hominid Sites in Africa," Vol. 1, "▶ Paleosols," Vol. 1, "▶ Quaternary Geology and Paleoenvironments," Vol. 1, "▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns," Vol. 1, and ▶ Modeling the Past: Archaeology, Vol. 1). Taylor (2002) also provides a useful recent summary of African ape diets. Within a highly variable context of local preferences and seasonal fluctuations and with considerable overlap in the fruits exploited, gorillas are, broadly speaking, more folivorous than chimpanzees. Gorillas consume less fruit than chimpanzees and exploit leaves, pith, bark, bamboo, and terrestrial herbaceous items. The eastern mountain gorilla (*G. g. beringei*) is the most exclusively folivorous form; the western lowland gorilla (*G. g. gorilla*) exploits the most varied diet, with a significant fruit component. In contrast, chimpanzee diets are dominated by fruits, although it is unclear whether the bonobo (*P. paniscus*) exploits more terrestrial herbaceous vegetation than the common chimpanzee (*P. troglodytes*) (Taylor 2002).

Compared with the orangutan, African apes exhibit longer, lower, narrower neurocrania set at a lower level relative to the facial skeleton (klinorhynchy). The frontal contour is low and retreating, the parietal region flat, and the occipital more curved than in the large-bodied Asian ape. There is a prominent supraorbital torus that is usually continuous across the glabellar region as well as above each orbit, although in some *P. troglodytes* individuals it may be divided by a slight depression. A supratoral sulcus, its lateral limits defined by the anterior temporal lines, delimits the torus from the frontal squama. The orbits are subrectangular, usually broader than high, and interorbital breadth is greater than in the orangutan, reflecting the broader ethmoid of African apes. On the medial orbital wall, the ethmoid's orbital plate is reduced, and the ethmolacrimal suture is usually much less extensive than in the orangutan and in some individuals may be replaced by contact of the interposed frontal and maxilla. There is an extensive frontoethmoid sinus (Fig. 4). On the floor of the anterior cranial fossa, the frontal may separate the ethmoid from the sphenoid, more commonly in *Gorilla* (>50 %) than *Pan* (15 %). Frontotemporal contact predominates on the lateral cranial wall of the chimpanzee and gorilla, but sphenoparietal contact is common in the bonobo.

The root of the maxillary zygomatic process arises relatively close to the occlusal plane, above M^1 or M^2. In the chimpanzee, the zygoma's facial (malar) aspect is limited in height and breadth; in the gorilla, it is deeper and extends further laterally. In both apes, it is remarkably thin in sagittal cross section when compared with most early hominins but is strengthened by the sagittal angulation of its upper and lower portions. Rak (1983) has emphasized the structural importance of the zygomatic region as a transverse buttress, linking the lateral and medial components of the face and resisting masticatory forces. In both gorilla and chimpanzee, the zygoma's temporal process is sharply angled from its malar surface, with the zygomatic arches orientated parasagittally/posteriorly slightly divergent (*Pan*) and parasagittaly/posteriorly slightly convergent (*Gorilla*), reflecting differing ratios of mid-facial and bitemporal breadths in the two genera. The greater facial breadth in *Gorilla* means that the masseters, especially their anterior fibers, have a greater lateral component to their contraction than in *Pan*.

The zygomatic arch is thin in cross section but vertically deeper, its inferior border marked anteriorly for the superficial masseter fibers, and in *Gorilla* posteriorly scalloped for the origin of the muscle's deeper portion. A part of this, sometimes differentiated as the *zygomaticomandibularis* muscle, fuses with anterior *temporalis* fibers, to attach to the *temporalis* tendon, the coronoid process, and anterior ramus edge (Raven 1950; Sakka 1984; Aiello and Dean 1990). In mature male gorillas, the arch is reinforced sagittally in its mid-region by a "step" with convex upper border which increases its vertical depth compared with immediately adjacent areas and strengthened transversely toward its rear by the broad, flat base of the temporal's zygomatic process. Additional support against the masseter's pull is provided by the *temporalis* fascia, inserting on the upper border of the zygomatic arch; again, it is particularly extensive in male gorillas.

Anteriorly the face is braced against masseteric force by the zygomatic buttress (see above) and by the beam of the supraorbital torus, which links with the zygoma via its frontal process (Rak 1983). The greater facial breadth of *Gorilla* combined with its more marked postorbital constriction and so deeper infratemporal fossa means that the lateral component of the torus is unsupported behind by the anterior neurocranial wall and so is massively thickened vertically and sagittally, while the postorbital bar is broadened compared with *Pan*. These structures, the canine roots, and nasal septum also reinforce the palate and face against bending (sagittal), torsional (coronal), and shearing forces generated during biting by the anterior teeth. Such forces are highest rostrally and of greatest magnitude in large-jawed forms such as *Gorilla* (Preuschoft et al. 1986).

Within the nasal cavity, the incisive canal is wide and the fossae are broad and bowl shaped. In *Pan*, the extent by which the premaxilla overlaps the palate, and so the length of the incisive canal, is comparable to that in the orangutan, although the canal is angled more steeply than in the latter because of the African ape's less convex premaxilla (Fig. 2 upper right). In *Gorilla*, the overlap is much less and the incisive canal shorter, and there is always a distinct step in the nasal floor between premaxilla and palate (Fig. 2 lower right). In *Pan*, the step is much less marked and may be absent altogether in about one third of individuals, who evince a smooth floor comparable to that of the orangutan (McCollum and Ward 1997). In *Gorilla*, a long prevomer is interposed between the vomer and the premaxilla, with the inferior parts of both the former bones descending into the incisive canal, dividing its posterior wall and eventually partitioning it into two channels. A septal groove along the nasal sill is seen only in younger individuals; in adults, it is confined to the rear of the sill. In *Pan*, the prevomer is much smaller, and, while it descends into the incisive canal to divide the posterior wall, together with the vomer, complete partitioning into two channels is much less frequent than in *Gorilla*. Unlike the latter, a septal groove is present on the nasal sill in adults as well as younger individuals.

Fusion of the facial aspect of the premaxillomaxillary suture in chimpanzees begins prenatally and is usually completed before the permanent dentition is fully erupted, with the nasal aspect being completely fused around the eruption of M^2. Facial growth in *Gorilla* continues for longer, with both facial and nasal aspects of the premaxillomaxillary suture and the prevomeral-vomeral sutures remaining open until well into maturity (McCollum and Ward 1997). Accessory premaxillary sutures are also quite common (>20 %) in *Gorilla*, indicating separate ossification centers for the palate and facial components of the premaxilla (Schultz 1950).

The palate is long in both *Pan* and *Gorilla*; externally it is shallow anteriorly with no clear alveolar border but deeper along the postcanine row. Internally, the maxillary palatine process of *Pan* is distinctive in thickening anteriorly and containing the palatine recess, a medial extension of the maxillary sinus. Laterally the maxillary alveolar process is thin, with the contours of the tooth roots evident;

medially the process is thicker. Rak (1983) argues that the maxillary zygomatic process acts as a mid-palatal buttress, reinforcing the hard palate against shearing stresses generated between the chewing and balancing sides of the dental arcade, primarily from the latter's medial pterygoid muscle. Both medial and lateral pterygoids are particularly well developed in *Gorilla*.

As in the orangutan, the preglenoid plane of African apes is long, the articular eminence only slightly developed so the glenoid fossa is sagittally shallow, and the postglenoid tubercle is well developed. The roof of the glenoid fossa is coronally more horizontal than in the orangutan and the entoglenoid more distinctly differentiated from it, especially in *Gorilla*, where it is very large, extending beyond the level of the articular eminence and preventing any medial shift of the condyle prior to moving onto the preglenoid plane (Du Bruhl 1977). In some of these features and in temporal bone shape overall, *Pan* is more derived than *Gorilla* (Lockwood et al. 2004). Terhune (2012) notes that joint surfaces in the mandibular fossa are sagittally extended in chimpanzees, whereas in gorillas the surfaces are sagittally contracted and in orangutans intermediate, and that much variation is associated with morphologies that promote gape rather than bite force. A prominent temporomandibular ligament is present in *Gorilla* and is apparently variably developed in *Pan* (Aiello and Dean 1990).

In *Pan* species, the dentitions are basically similar, although *P. paniscus* teeth are smaller and less sexually dimorphic than those of *P. troglodytes*. A comparative study of root length development (Dean and Vesey 2008) revealed that in *P. troglodytes*, anterior tooth root growth rose quickly to higher rates and then plateaued, with the highest rates in canines, followed by incisors (the reverse of the *H. sapiens* pattern). In both modern humans and apes, molar tooth roots grew in a nonlinear pattern, with peak rates reducing from M1 to M3. A recent study (Boughner et al. 2012) showed no significant differences in the relative timing of permanent tooth crown and root formation in bonobos and chimpanzees. Similarly, dental topographic analyses that reflect contrasts in occlusal form related to diet among primate species identified differences between wear stages within subspecies in surface slope, relief, and angularity, but failed to differentiate between *Pan* subspecies (Klukkert et al. 2012). Discriminant analysis of size transformed and untransformed molar traits (Pilbrow 2006), however, yielded more effective separation (see below).

Smith et al. (2010) present data on crown and root formation in Taï Forest chimpanzees to evaluate claims that wild chimpanzees display delayed dental development compared with captive ones. They conclude that crown formation onset and development markedly overlap captive chimpanzees, whereas root development may be accelerated in captive specimens, and wild individuals fall near the middle or latter half of captive eruption ranges. Overall the authors conclude that while minor developmental differences are evident in some comparisons, the results do not show a consistent pattern of slower tooth formation in wild individuals. A later paper (Smith and Boesch 2011) extends the analysis to estimate that delayed tooth emergence in wild individuals is more moderate than previously recorded, averaging about 1 SD of the captive distribution, rising to 1.3 SD if age estimate criteria are relaxed; M_1 emergence is estimated at 3.66–3.75 years in wild chimpanzees. The authors point out that "wild" data are usually skewed, often deriving from diseased, debilitated, or otherwise pathologically affected corpses of immatures, who cannot be considered fully representative of a healthy population.

The maxillary incisors are curved mesiodistally, with I^1 larger than I^2, although the difference is smaller in *P. paniscus* than in *P. troglodytes*. In the mandibular incisors, these proportions are usually reversed. The upper canine is larger in males than females of both species; its mesial surface is more convex in *P. troglodytes* and, with the lingual surface, displays grooving absent in a small sample of *P. paniscus* (Swindler 1976). In the upper jaw, M^1 and M^2 are subequal in size, M^3 reduced, with the hypocone the smallest cusp and reducing progressively along the molar row. Reduction is more pronounced in *P. paniscus*, and the cusp may even be completely absent from M^1 and M^2 in some individuals, whereas it is always present on those teeth in *P. troglodytes*. The hypocone may be entirely absent on some M^3s of both species but is more weakly developed in bonobos (fully developed in 21 % of *P. troglodytes* teeth, compared with only 9 % of *P. paniscus*). The preprotocrista (anterior transverse crest between paracone and protocone) is more angled and transversely orientated in *P. paniscus*, running from closer to the protocone to mesial of the paracone rather than to its tip, as in *P. troglodytes*. The distoconule, an accessory cusp between hypocone and metacone, is absent in bonobos but present in all chimpanzee subspecies, generally at low frequency but up to 40 % of M^3 in one collection of *P. t. troglodytes* (Kinzey 1984). A lingual cingulum is often present, most frequently on M^1 but larger on M^3 and better developed (longer distally) in bonobos than chimpanzees.

M_2 is usually the largest mandibular molar, M_3 the smallest; a Y-5 cusp pattern is almost universal on M_1 but only occurs in <50 % of cases on M_3. The talonid is extensive, and a buccal cingulum is rarely (5–10 %) present (Swindler 1976). In *P. paniscus*, the metaconid is usually opposite the protoconid rather than distal to it as in *P. troglodytes*, resulting in a greater relative distance and a deeper groove, between the metaconid and entoconid in the former species (Kinzey 1984). Nonetheless, the two cusps are closely adjacent compared with *Gorilla*. The hypoconulid is usually slightly buccally positioned in chimpanzees and more centrally (lingually) placed in bonobos, while a tuberculum sextum is often present between hypoconulid and entoconid in the former species but more rarely in the latter, which Kinzey (1984) suggests may be associated with the more lingually positioned hypoconulid. *Pan* molars are often wrinkled but not to the extent seen in *Pongo*. Skinner et al. (2009) demonstrated that shape contrasts in the enamel-dentine junction of M_1 and M_2, especially in the relative height and position of the dentine horns, dentine crown height, and the shape of the base, serve to differentiate *Pan* species and subspecies, so extending the utility of teeth with worn occlusal surfaces for systematic identification.

Central to lateral incisor proportions in *Gorilla* are comparable to those of *Pan*, although compared to the postcanine teeth, the incisors are much smaller. Canines are large and markedly dimorphic, in the female projecting less beyond the other teeth. Contrary to the sequence in *Pan*, but like the orangutan, P_4 erupts before P_3, which is sectorial but with a vestigial metaconid, a large distal fossa for the P^3 protocone, and a well-developed lingual cingulum. On the upper molars, the hypocone is larger relative to the other cusps than in other apes; the mesial fossa is narrow, the distal one wide, and a lingual cingulum is usually present. On the lower molars, the metaconid and entoconid are widely separated, and there is an extensive talonid basin to receive the large protocone of the upper molar. A tuberculum intermedium is often present between metaconid and entoconid on M_1 and is almost invariably so on M_2 and M_3; a tuberculum sextum may also occur between the entoconid and the buccally positioned hypoconulid. A buccal cingulum is usually present on M_1, on about 50 % of M_2, and on a minority of M_3; overall, it is both more common and better developed in *Gorilla* than in other extant apes. In the upper jaw, M^2 is usually the largest tooth; in the lower jaw, M_1 is the smallest, with M_2 and M_3 subequal (Swindler 1976). Dimorphism in dental dimensions is extensive in *Gorilla*, with most teeth differing significantly in size between the sexes. Tooth enamel is smooth, without the wrinkling displayed by *Pongo* and *Pan*. Supernumerary molars may occur, more often in the upper jaw than the mandible.

McCollum (2007) investigated the relationships of diet, incisor wear, and incisor crown breadth in western lowland gorillas and chimpanzees, confirming that incisor dimensions are broadly similar in the two apes. She found that incisor wear was greater in the more folivorous gorilla than in the frugivorous chimpanzee, questioning Hylander's suggestion that larger incisors and enhanced resistance to wear are associated with frugivory and the need for greater incisal processing of large fruits. Using a more extensive database, however, Deane (2009) has demonstrated that increased mesiodistal incisor length and greater incisor crown curvature are correlated with greater frugivory, so reaffirming Hylander's proposed link. Hard-object frugivores show greater curvature than soft-object frugivores, while mixed folivores/frugivores display intermediate degrees of curvature compared with frugivores and folivores. Frugivores also have mesiodistally wider I_1, I_2, and I^2 crowns relative to their labiolingual lengths, while folivores have labiolingually broader crowns than mixed folivore/frugivores, and those of hard-object frugivores are broader than those of soft-object frugivores. McCollum and Deane's conflicting findings may result from their differing databases – two species with overlapping diets in McCollum's study compared with a larger number of taxa and wider dietary spectrum in Dean's case – and in their scaling to adjust for body size differences.

Cray et al. (2008) have shown that cranial vault suture closure mirrors consensus phylogeny, with *H. sapiens*, *P. troglodytes*, and *G. gorilla* sharing a similar lateral-anterior closure pattern, while *G. gorilla* displays a distinct vault pattern that follows a strong posterior to anterior gradient. *P. troglodytes* is thus more like *H. sapiens* in suture synostosis, in accord with these two species sharing a common ancestor after the *Gorilla* clade split off. *P. paniscus* was not included in the analysis.

Temporal muscles are well marked on the cranial walls in the chimpanzee, often forming raised ridges which in mature males may occasionally meet to form a sagittal crest. In male gorillas, a pronounced sagittal crest is present, thickened at the top where the two temporal laminae abut, and highest toward the rear of the vault where it unites with the nuchal crest, forming a beak-like posterior projection at the rear of the skull. The crest, besides enlarging the area for *temporalis* attachment, improves the power of the cheek teeth by increasing the relative length of the muscle insertion axis compared with the load and also serves to increase the effective height of the neurocranium, thereby enhancing its resistance to the vertical forces generated during mastication (Davis 1964).

A compound T/N crest (Robinson 1958) forms laterally in chimpanzees from the juxtaposition of the temporal and nuchal muscles, but these diverge medially, and there the perimeters of the temporal and nuchal muscles are marked by lines, slightly raised ridges, or a simple nuchal crest. In male gorillas, the nuchal muscles develop medially as well as laterally beyond the neurocranium proper, producing a compound T/N crest uniting with the sagittal crest as above and resulting in an extensive, triangular-shaped nuchal area.

Temporalis fibers originate from the lower part of the nuchal crest's anterior surface but do not attain its rim, which provides attachment for the *occipitofrontalis* scalp muscle (Sakka 1984; Aiello and Dean 1990). Medially *trapezius* and laterally *sternocleidomastoideus* insert on the posterior rim of the nuchal crest, with below these the rhomboids (medially), and the fleshy, laterally extensive *splenius capitis* muscles. Deep to these is the heavy *semispinalis capitis*, which may be divisible into medial, thick biventer, and more lateral, straplike, complexus portions (Aiello and Dean 1990), although this separation is said to be uncommon in *Pan* (Swindler and Wood 1973) and is not indicated in Raven's (1950) account of *Gorilla* anatomy.

On the cranial base, *rectus capitis lateralis* lies immediately lateral to the mid-rear portion of the occipital condyle in *Gorilla* and *Pongo* and to the front mid-portion of the condyle in *Pan* (Dean 1984; Raven 1950). It is unclear whether the rather more anterior insertion of the muscle in the chimpanzee reflects individual variation or a specific trait. Just lateral and slightly posterior to this muscle is the digastric; see above for its distinctive form in the orangutan. Just in front of the foramen magnum and close to the midline are the closely adjacent *rectus capitis anterior* muscles, and ventral to these the *longus capitis* muscles. The basilar suture fuses early in the African apes and the orangutan, severely limiting its utility for determining individual age (Poe 2011).

Nishimura et al. (2006) have documented vocal tract growth and development in three chimpanzees. In early infancy, they show rapid laryngeal descent with consequent changes in vocal tract proportions as a result of descent of the laryngeal skeleton relative to the hyoid. Subsequently, the hyoid also descends relative to the palate, maintaining rapid laryngeal descent, as in humans. They conclude that descent of the larynx evolved before the *Pan*-hominin split for a function unrelated to speech and that human speech capabilities resulted from facial flattening rather than laryngeal descent.

Individual Species Morphology and Intraspecific Diversity

Pan

Pan troglodytes

The commonly recognized subspecies may be distinguished cranially as below, based primarily on Groves (2001).

P. t. troglodytes possesses a very broad head combined with a comparatively narrow muzzle, a continuous, straight, medially thickened supraorbital torus, more concave facial profile, and more gradually sloping occipital than other subspecies. On the medial orbital wall, ethmo-lacrimal contact is very common, while supernumerary bones on the lambdoid suture are rare, as are multiple infraorbital foramina.

P. t. verus also has a broad, rather flat-topped cranium but a broader muzzle, a less sharply concave facial profile, and a more steeply curved occipital. The supraorbital torus is arched over each orbit and is laterally well developed. Ethmo-lacrimal contact is very rare, while additional bones at lambda and along the lambdoid suture are very common. The frequency of a single infraorbital foramen bilaterally is higher than in other subspecies.

P. t. schweinfurthii has a more rounded skull than other subspecies, with an elongated, gently sloping occipital. The facial profile tends to be straight or only slightly concave, and the muzzle narrow, although interorbital breadth is high. The straight, continuous supraorbital torus is thinner than in other subspecies, especially laterally, but is prominent at glabella. Multiple infraorbital foramina are very common, and frontotemporal contact at pterion virtually universal. In cranial nonmetric traits, generally it resembles *P. t. troglodytes* but is rather smaller and less sexually dimorphic than that subspecies. Despite this, Angst (quoted in Groves et al. 1992) has reported a higher average cranial capacity for *P. t. schweinfurthii* – 420 cm^3 – compared with virtually identical capacities for *P. t. troglodytes* and *P. t. verus* (401 and 404 cm^3, respectively). Highly variable in size and cranial proportions, *P. t. schweinfurthii* may incorporate more than one subspecies.

P. t. vellerosus is a recently recognized subspecies from Nigeria to Cameroon (Gonder et al. 1997), identified on mtDNA sequencing that showed it to be a sister taxon of *P. t. verus*. Cranially it is unlike *P. t. verus* but similar to *P. t. troglodytes* and *P. t. schweinfurthii* in its high frequency of ethmo-lacrimal contact and low frequency of Wormian bones at lambda and along the lambdoid suture (Groves 2001).

A study of chimpanzee molar development (Smith et al. 2007) indicated marked within cusp, between cusp, and between tooth variation in enamel formation times and in cuspal initiation and completion sequences, pointing to the need to take account of significant variation when interpreting hominoid and hominin developmental data. In contrast, discriminant analysis of upper and lower molar morphometrics (Pilbrow 2006) to assess the efficacy of dental evidence in distinguishing chimpanzee populations differentiated on geographical criteria (river boundaries) provided more consistent findings. The results showed clear distinction of *P. paniscus* (see below) and *P. troglodytes* at all molar positions, while within the latter *P. t. verus* was distinct from other *P. troglodytes* populations, *P. t. vellerosus* was also clearly differentiated, and *P. t. troglodytes* and *P. t. schweinfurthii* were dentally similar.

Pan paniscus

Bonobos are characterized by relatively smaller heads and teeth than common chimpanzees, but by comparably sized upper limbs, rather lighter, more slender trunks, and heavier hind limbs (Susman 1984; Zihlman 1984). The bonobo skull is smaller, smoother, and more lightly built than that of the chimpanzee, the mandible appreciably shorter, and the face considerably less prognathic and reduced in height (Fig. 5). Reflecting the less projecting face and jaws, the cranial base is more tightly flexed, with a mean angle of 140° compared with 145° in the chimpanzee (Cramer 1977). This flexion results from a basicranial growth pattern to adulthood in *P. paniscus* that resembles that of *P. troglodytes* curtailed at the subadult (M^2 eruption) stage (Laitman and Heimbuch 1984; see also below). The bonobo supraorbital torus is thinner and the supratoral sulcus weaker, while the frontal squama rises (and the occipital descends) more steeply than is usual in *P. troglodytes*. It is more common (57 %) for the sphenoid and parietal to suture at pterion (contrast *P. troglodytes* above), while on the orbital wall frontomaxillary contact is more frequent than in chimpanzees (24 % and 9 %, respectively, Cramer 1977). Following CT scanning, Balzeau et al. (2009a, b) provide further information on the type specimen of *P. paniscus*, including details of its internal cranial anatomy.

While bonobos exhibit some canine dimorphism, there are only very limited differences between sexes in the size of the incisors and cheek teeth (see above). Similarly, mean endocranial capacity is virtually identical in males and females at c. 350 cm^3 compared with 404 and 375 cm^3, respectively, in *P. troglodytes* (Cramer 1977). The nuchal area may be bounded by a low ridge or line, but a true crest with sharply defined rim is absent, as is any sign of sagittal cresting. Consistent with its more neotenous form, *P. paniscus* shows earlier closure of the facial component of the premaxillary/maxillary suture than *P. troglodytes* and much higher frequency of a completely open palatal component (>93 % cf. 19 %, respectively, of individuals with M^1 erupted; Braga 1998). This early synostosis results in a vertically and horizontally shorter face and reduced dental arch, consistent with the bonobo's significantly smaller incisors, compared with *P. troglodytes*. Kinzey (1984) notes the greater degree of incisor wear in *P. paniscus* than *P. troglodytes*, which he suggests may be related to a greater incidence of pith and leaf petioles in the diet; he also speculates that the combination of a more transversely orientated and angled preprotocrista, with a more mesially sited metaconid and deeper groove between protoconid and hypoconid into which the crest occludes (see above), produces a more efficient shearing mechanism that again may reflect a more folivorous dietary component in bonobos.

Comparison of small samples of immature captive and wild female *P. paniscus* with *P. troglodytes* showed similar patterns of skeletal fusion in the two captive groups with the pattern of tooth eruption to bone fusion also generally consistent between species save for minor variations in late juveniles and subadults. While displaying similar patterns, direct age comparisons showed skeletal growth in the captive bonobo group to be accelerated compared with both captive and wild *P. troglodytes* samples (Bolter and Zihlman 2012).

Morphometric studies illustrate the relative homogeneity of chimpanzee cranial form compared with other great apes. While usually distinguishing *P. paniscus* from *P. troglodytes*, differentiation within the latter is, not unexpectedly, less secure, with extensive overlap between subspecies; see, for example, Shea and

Coolidge (1988). These authors found that discrimination just about reached the subspecies threshold and that separation was considerably less than in orangutans or gorillas (see below). They considered that this comparative uniformity might reflect a more recent differentiation of *P. troglodytes* subspecies, more frequent or extensive contact – and so gene flow – between them, marked ecological flexibility for the species overall so precluding close matching of subspecific features to habitat, or any combination of these. A subsequent study (Groves et al. 1992), with specimens sorted by location rather than subspecies, produced neither meaningful geographic patterning nor subspecific grouping among males. Female crania, however, exhibited better separation, with *P. paniscus* distinct, *P. t. schweinfurthii* grading geographically toward *P. t. troglodytes*, and with evidence for east–west differentiation within *P. t. schweinfurthii* based on facial proportions.

Shea et al. (1993) compare the results of both raw and size-adjusted analyses. For the former, there is 100 % correct classification for *P. paniscus* females and about 75 % correct classification for *P. troglodytes*, of which *P. t. verus* and *P. t. schweinfurthii* are furthest apart, according with their geographic separation. Confining the analysis to *P. troglodytes*, however, removes this geographic gradient, with maximal separation now between *P. t. troglodytes* and *schweinfurthii*. As expected, size adjustment reduces separation of *P. paniscus* from *P. troglodytes*, so that the distance between *P. t. verus* and *P. t. schweinfurthii*, now the most widely divergent subspecies, approaches that between the latter and *P. paniscus*. Principal Components Analysis shows *P. paniscus* clustering with immature *P. troglodytes* crania along PC 1, indicating their common growth trajectories and emphasizing that shape contrasts between bonobo and chimpanzee reflect the smaller size and truncated growth of the former relative to the latter, within which the major differences between *P. t. troglodytes* and *P. t. schweinfurthii* are also due to size and associated allometric factors (see below).

Separate analysis of mandibular variation in *Pan* accords generally, but not completely, with the above (Taylor and Groves 2003). Mandibular separation within *P. troglodytes* is less than that within *Gorilla*, but contrasts between *P. paniscus* and *P. troglodytes* are greater than *Gorilla*, and there is clear separation of bonobos and chimpanzees. There is extensive overlap of *P. troglodytes* subspecies, maximally between *P. t. schweinfurthii* and *P. t. troglodytes*, and greatest distinction between the latter and *P. t. verus* (contrast to Shea et al.'s cranial finding of greatest overlap between *P. t. troglodytes* and *P. t. verus*). Size adjustment again reduces separation, so that bonobos, while remaining the most distinctive, now partly overlap with chimpanzees; and *P. t. verus*, while still the most isolated of chimpanzee subspecies, is now furthest from *P. t. schweinfurthii* (as on the cranial data). *P. t. verus's*; distinctiveness on mandibular traits, while relatively slight (Taylor and Groves 2003), nonetheless accords with Braga's finding (1998) that premaxillomaxillary suture closure differs significantly between *P. t. verus* and other subspecies, with *P. t. verus* displaying later complete closure of the suture's facial component and earlier closure of its palatal component compared with *P. t. troglodytes* and *P. t. schweinfurthii* (Braga 1998). This points to a longer, deeper lower face in *P. t. verus* than other subspecies.

A recent morphometric study of mandibular form (Robinson 2012) broadly accords with Taylor and Groves' findings: size-adjusted corpus shapes in *P. paniscus* and *P. troglodytes* could be assigned with 93 % accuracy, with much of the shape differences size related, but subspecies could only be correctly identified <75 % of the time. Robinson's findings indicate symphyseal shape to be especially informative in distinguishing *Pan* species, with potential implications for hominin systematics.

Zihlman et al. (2008) present cranial and postcranial data on 25 *P. t. verus* individuals of known age and sex from Taï National Park, Cote d'Ivoire, and compare them with a *P. t. schweinfurthii* sample from Gombe National Park, Tanzania, with *P. paniscus* as an additional comparator. Taï males and females differ in cranial capacity and, as do the Gombe sexes, in facial dimensions. The Tai sample has a smaller cranial capacity, longer palate and mandible, and greater trunk dimensions and limb lengths; most variation is in females, with males differing only in humeral and femoral lengths. A further study by Neubauer et al. (2012) of endocranial volumes (EV) in an ontogenetic series of Taï forest chimpanzees showed brain size to increase rapidly during early ontogeny and for sexual dimorphism in EV, with males larger than females, to be evident before adult EV was attained. The mean adult EV in this Taï Forest sample was just under 380 cm^3.

Gorilla

Most accounts of *Gorilla* cranial diversity are based on Groves' highly influential morphometric analysis of variation in 45 traits from >700 gorilla skulls, grouped by origin into 19 and 10 geographic localities for crania and mandibles, respectively (Groves 1967, 1970). D^2 values were calculated for each of the ten cranial and six mandibular representative variables, allowing the localities to be grouped into eight larger regions which could be further combined on the basis of intra- and intergroup differences into three clusters: a relatively homogeneous western cluster (four regions, of which the Cross River sample was rather more distant from the other three), a distinctive eastern group from the Virunga volcano region, and a further eastern group (three regions). These correspond to the western lowland gorilla (*G. g. gorilla*), the eastern highland gorilla (*G. g. beringei*), and the eastern lowland gorilla (*G. g. graueri*) (Fig. 6).

G. g. gorilla is the smallest subspecies, with fairly broad face, small jaws and teeth, a short palate, a single mental foramen under P_3 or P_4 (more usually under the latter), and a jaw condyle without a cleft. *G. g. graueri* is the largest subspecies, with a high, narrow face; larger jaws and teeth; and a longer palate. The mental foramen is often multiple and set under P_3, while the jaw condyle is often cleft. The mountain gorilla, *G. g. beringei*, is distinguished by a low, broad face; very large jaws and teeth; a very long tooth row and palate; anteriorly sited (under C or P_3) multiple mental foramina; and a jaw condyle that is usually cleft.

Stumpf et al. (1998), adjusting for size, demonstrated that the Cross River sample was more distinctive than Groves' original analyses indicated, so providing support to the growing movement advocating its recognition as a further subspecies, *G. g. diehli* (see Sarmiento and Oates 1999, 2000; Groves 2001, 2003). *G. g. diehli* is distinguished by its shorter skull, shorter molar row, narrower palate, shorter cranial base, and more steeply angled nuchal plane than other western gorillas, which Sarmiento and Oates speculate may be associated with a diet of smaller, drier, and harder food items than that of other western gorillas.

A further reanalysis of Groves' data (Stumpf et al. 2003) confirmed a primary east–west separation on the latter's smaller values for palatal and tooth row lengths, nasal aperture and nasal bone breadths, lateral facial height, and supraorbital torus thickness. They also demonstrated the distinctiveness of the Cross River and Virunga populations from other west and eastern groups on the basis of their narrower interorbital breadths, narrower palates, and reduced lateral facial height. Analyses restricted to the western populations further indicate the distinctiveness of *G. g. diehli* on overall and neurocranial lengths, bicanine and bimolar breadths, interorbital and neurocranial widths, palatal length, and medial and lateral facial heights. Stumpf et al., however, emphasize that the fundamental distinction is between east and west *Gorilla* populations, with the corollary that *G. g. graueri* is more closely related to *G. g. beringei* than it is to western lowland gorillas. The implications of this, together with recent data from molecular and other studies, have led Groves (2001, 2003) to revise his earlier taxonomy and to differentiate western and eastern gorillas at the species level as *G. gorilla* (*G. g. gorilla* and *G. g. diehli*) and *G. beringei* (*G. b. beringei* and *G. b. graueri*), respectively. This also accords with the zoogeographical evidence, but for consistency with other sources referred to herein, we retain the traditional single species classification.

Leigh et al. (2003), however, apply Wright's F_{ST} (an indicator of microdifferentiation, measuring the extent to which subdivision within species – i.e., between subspecies – departs from random mating) to Groves' craniometric data and to discrete trait variation and reach different conclusions. Their approach requires assumptions about population sizes and the heritability of craniometric traits but is considered to be robust, especially, when subspecies sizes differ markedly, as they do in *Gorilla*. F_{ST} calculated from the craniometric data yields unexpectedly low levels of between group variation, only c. 20 % between subspecies compared with 80 % within subspecies assuming equal population sizes. Adjusting for different population estimates between the subspecies results in even lower values of F_{ST}, with correspondingly more variation within subspecies. F_{ST} derived from discrete trait analysis gives rather higher, but still modest, levels of divergence. Leigh et al. argue that much gorilla variation reflects ontogenetic changes and sexual dimorphism, and as such is intra-subspecific, and that their results offer no support for differentiating eastern and western gorillas at the specific level. See also Albrecht et al. (2003) for a detailed analysis of *Gorilla* cranial diversity at locality, deme, subspecies and species levels, and its potential evolutionary and sociobiological implications. Interestingly, genetic data indicate much deeper levels of differentiation among African ape species than the morphological evidence does (Gagneux et al. 1999; Lockwood et al. 2004).

Caillaud et al. (2008) explore the possible sociobiological basis for sexual dimorphism – specifically male body size and head crest development – in *G. g. gorilla*, through photogrammetry and field observations. Their findings show the number of females belonging to a mature male correlates with head crest size, body length, and musculature and that female numbers at male-male encounters, where larger individuals could be expected to be at an advantage, strongly affect the number of male agonistic displays. Exaggerated male traits therefore convey a mating advantage, whether through male-male fighting or female mate choice. Similar drivers may well be influencing the evolution of dimorphism in other, larger-bodied gorilla taxa.

Breuer et al. (2012) also explored the relationships of body length, crest size, and gluteal muscle size with long-term male reproductive success in western gorillas. They found that all three traits correlated with the average number of mates per male, but that only crest size and gluteal development significantly correlated with offspring survival and the annual rate of siring offspring who survive to weaning.

Dental variation in *Gorilla* is considerable: molar shapes and cusp proportions, relatively invariant within subspecies, differ between subspecies, as do tooth dimensions (Uchida 1998a). Male (but not female) *G. g. beringei* canines are larger than those of *G. g. gorilla* and *G. g. graueri*. In the postcanine dentition, *G. g. graueri* is, surprisingly, significantly larger than *G. g. beringei*, which is larger than *G. g. gorilla*. While upper molars of *beringei* show B-L enlargement, those of *graueri* are expanded in both length and breadth. *G. g. gorilla* has wider incisors relative to molar length than the eastern subspecies, while *G. g. beringei* displays higher crowned cheek teeth with sharper cusps and ridges than *G. g. gorilla*. *G. g. graueri* has a relatively smaller talonid on P_4 and, together with *G. g. beringei*, has larger distal cusps on the upper and lower molars than *G. g. gorilla*. Patterns of dental sexual dimorphism differ among gorilla subspecies: *G. g. beringei* displays greatest dimorphism in canine and lower molar size, *graueri* greatest dimorphism in upper molars, with *G. g. gorilla* least dimorphic both in canines and molars. This reflects a larger canine relative to molar size in females of this subspecies, which Uchida considers to reflect heightened female-female competition, possibly related to greater frugivory. She stresses the importance of local dietary adaptation influencing tooth form and proportions, with considerable variation but with more extensive frugivory in *G. g. gorilla* and lowland *G. g. graueri* than in highland populations of that subspecies and *G. g beringei*.

Similarly, Pilbrow (2010) has analyzed molar morphometrics to assess gorilla geographical diversity. Her results support species distinction between *G. gorilla* and *G. beringei*, with subspecies *G. g. diehli*, *G. g. gorilla*, *G. b. graueri*, *G. b. beringei*, and a possible further subspecies, *G. b. rex-pygmaeorum*; dental metrics thus accord with other evidence for gorilla population diversity. Dental separation increased with altitude differences but not geographical distance, so that altitudinal segregation better explains gorilla population divergence better than isolation by distance. Pilbrow argues that the historic center of gorilla distribution was West Africa and that Plio-Pleistocene climatic oscillations combined with mountain building promoted drift and population differentiation. Further analyses of the gorilla masticatory system are discussed below.

Allometric and Biomechanical Studies

The greater size of the gorilla relative to the chimpanzee is an instance of peramorphosis (Shea 1983c). Length of maturation is comparable in all three African ape species, but gorillas grow much more rapidly and to greater sizes than chimpanzees, while bonobos grow somewhat more slowly than chimpanzees (rate hypermorphosis) to rather lesser sizes (although there is considerable overlap); within each species, males grow for longer than females (time hypermorphosis). The pattern indicates that the interspecies differences reflect selection for greater body size, perhaps associated with increasing terrestrial folivory rather than selection for delayed maturation (Shea 1983c).

Significant differences between *Pan* and *Gorilla* growth in body weight only become apparent after about 2 years, with gorillas pulling away increasingly strongly from the chimpanzee growth curve thereafter (Shea 1983d; Fig. 6). Since neural growth is predominantly prenatal/immediately postnatal, there is no corresponding increase in *Gorilla* brain size in later ontogeny; the natural consequence is that, while having absolutely larger brains than chimpanzees, gorillas have lower brain–body ratios and lower encephalization quotients, with male value particularly depressed compared with females. “In the case of the African pongid species . . . the developmental pathway utilized to increase body size ensures that relative brain size decreases as a consequence” (Shea 1983d, p 58). It follows that attempted explanations of behavioral and/or ecological contrasts between the species based on differences in relative brain size should be regarded with skepticism.

Shea (1983a, 1984) also summarizes evidence that the differences in body form between adult *P. troglodytes* and *P. paniscus* result from ontogenetic scaling. The extension of common growth allometries to different end sizes holds within the skull, trunk, and limbs but not between them, so that adult bonobos do not match any single stage in chimpanzee ontogeny. Relative to the latter, the *P. paniscus* skull is most strongly reduced in size, forelimbs and trunk less reduced, and hind limbs not reduced at all, so that for a given body size, *P. paniscus* has a smaller skull than *P. troglodytes*. This is turn results in a more paedomorphic cranial shape compared with the chimpanzee through the decoupling of growth rates for the head and body, with the former slowed relative to the latter – an instance of neoteny. The selective factors underlying this process are obscure, although Shea speculates that the reduced sexual dimorphism and different social organization of *P. paniscus* compared with *P. troglodytes* may be important drivers in the evolution of its distinctive cranial proportions.

A more recent morphometric study by Lieberman et al. (2007) also concluded that the bonobo skull is largely paedomorphic relative to the chimpanzee, but that not all shape differences between the species, particularly in the face, could be explained in such terms, and that other developmental differences were also responsible for the contrasts in form. Durrleman et al. (2012) document ontogenetic changes in endocranial size and shape in sizeable samples of *P. paniscus* (n = 60) and *P. troglodytes* (n = 59) aged on dental criteria. They identify in bonobos an early, strong anisotropic endocranial expansion and bending due to localized expansion of the frontal pole, occipital lobe, and superior parietal lobe, which contrasts with developmentally later endocranial expansion in the chimpanzee. Patterns of expansion also differ in magnitude between the species, with a phase of rapid increase in endocranial volume occurring later in chimpanzees than bonobos.

Earlier suggestions (Ackermann and Krovitz 2002) of a common cranial postnatal ontogenetic shape trajectory or of separate but parallel shape trajectories that merely accentuate differences established in early (prenatal) ontogeny have been refuted by Cobb and O'Higgins (2004), who show hominin postnatal shape trajectories to be divergent with differing shape changes between species, even in early postnatal ontogeny (Vidarsdottir and Cobb 2004). The directions of scaling trajectories between *Pan* species, however, are not significant (so changing postnatal facial shape in a similar manner from different starting points), whereas those between *Pan* and *Gorilla* are directionally distinct.

Cobb and O'Higgins (2007) explore the role of ontogenetic scaling in determining sexual dimorphism in the facial skeleton of African apes (*G. g. gorilla*, *P. paniscus* and *P. troglodytes*). Using geometric morphometric analysis, they found that on average males and females shared a common ontogenetic shape trajectory and a common ontogenetic scaling trajectory until around M2 eruption. Thereafter, males and females diverged from each other and from the common juvenile trajectories within each species, indicating ontogenetic scaling as a mechanism until around "puberty" and the development of secondary sexual characters, but that subsequent sexual dimorphism occurs through divergent trajectories and not via ontogenetic scaling.

In general, the degree of adult cranial sexual dimorphism is greater in the larger apes (gorilla and orangutan) than in the chimpanzee and bonobo. *Gorilla* males display more size and shape *variability* than females, and a similar difference appears to be present in *Pongo*, but not in *Pan* (O'Higgins and Dryden 1993). Most of the differences reflect greater male facial prognathism, in turn a consequence of canine dimorphism. Adult cranial dimorphism appears to result from distinct mechanisms in the African and Asian apes. Whereas in *Pan* and *Gorilla* cranial dimorphism follows from extending the growth period of males for most cranial proportions (Shea 1983c), in *Pongo* only about half the growth allometries exhibit this process, with the other half displaying accelerated growth in males compared with females (Leutnegger and Masterson 1989a, b).

Male and female chimpanzees display significant cranial size differences but no shape differences, perhaps because the period of extended growth is a short one and/or the scaling coefficients are minor, so resulting in insignificant shape differences given the comparatively modest size of chimpanzees. As with the bonobo-chimpanzee comparison above, these differing patterns of cranial dimorphism in the great ape genera have been linked to socioecological contrasts between them (O'Higgins and Dryden 1993); see also Caillaud et al. (2008) and above.

Shea has also explored allometric influences on African ape craniofacial and dental form and their relationships to diet using bivariate and multivariate techniques. Many facial proportions in the bonobo, chimpanzee, and gorilla exhibit ontogenetic scaling, i.e., a common pattern of size/shape change. There are also instances, however, where this does not obtain: for example, chimpanzees have shallower zygomatic roots, narrower bizygomatic breadths, smaller infratemporal fossae, and narrower anterior cranial bases than bonobos with the same basicranial lengths. In other words, these features are reduced in chimpanzees compared with the values expected in bonobos ontogenetically scaled to their sizes (Shea 1984). Similarly, in those features in which chimpanzees are reduced relative to bonobos, gorillas tend to be reduced relative to chimpanzees (Shea 1984). As Shea points out, such allometrically adjusted analyses point to the opposite conclusion from that usually drawn from the study of absolute skull sizes – cranially; bonobos are relatively the most robust, and gorillas relatively the most gracile of the African apes.

Additionally, gorillas have significantly longer and higher cranial vaults, higher orbits, and longer foramen magnums than chimpanzee crania of equivalent basicranial lengths. They also exhibit longer, more projecting nasal regions that are sited lower on the face, than comparably sized chimpanzees. As overall skull size increases in the sequence bonobo-chimpanzee-gorilla, the three species also exhibit relatively narrower faces and neurocrania, reflecting in the latter case, the fact that increased brain size results primarily from growth in length, not width, during the prenatal and early postnatal phases.

During late postnatal growth, occipital length and breadth in gorillas increase appreciably compared with chimpanzees, reflecting the development of sagittal and nuchal crests as a functional response to the enlarged temporal and nuchal muscles "outgrowing" their areas of attachment on the exterior cranial wall. This, in turn, is a consequence of the respectively positive and negative allometric relationships between splanchnocranial and neurocranial proportions and body size. Dental metrics indicate that gorillas have relatively smaller incisors and relatively larger cheek teeth than comparably sized chimpanzees, while, surprisingly, temporal fossa area (and so temporal muscle size) becomes relatively smaller across the three species as size increases. Despite these differences, the predominant pattern among the African apes is essentially one of similarity in craniofacial growth. Multivariate analysis yields a common allometry vector incorporating $>93\ \%$ of total variance confirming this general picture, with a second vector (3.4 %) distinguishing chimpanzees and gorillas.

Shea considers that the differences in midface proportions between *Pan* and *Gorilla* may reflect differences in soft-tissue function or dietary contrasts, although the influence of the latter is by no means clear. In fact, he notes that while dental contrasts between the two apes can fairly clearly be linked to diet, no significant reorganization of the face occurs, with its form being primarily determined by the endpoints of common allometric trajectories. This suggests that the face and masticatory apparatus may be less strongly coupled to diet than is the dentition and/or that chimpanzee and gorilla diets, while differing in their constituent items, may not differ appreciably in their physical properties, in particular the force required to process them. For Shea, the African ape masticatory complex provides an example of an integrated functional system preadapted to extension into new size ranges and dietary shifts.

Molar crown area scales positively in hominoids, so that larger forms have relatively as well as absolutely larger crown areas, associated with their generally increased folivory, primarily achieved through increased tooth lengths rather than breadths (Demes et al. 1986). There are associated increases in palatal and mandibular lengths and relative narrowing of upper and lower dental arcades in larger taxa. Allometrically determined snout elongation produces greater bite force in larger animals, by lengthening the horizontal distance between the mandibular joint and the molar row, which Demes et al. have shown scales with a mean value of c. +1.6 in hominoids. Bite force is maintained by lengthening the masticatory muscles' power arms, by increasing their cross-sectional area, or by a combination of these. The temporal muscle's power arm scales from +1.16 (male great apes) to +1.62 (female gibbons) and that of the masseters and medial pterygoids, which is strongly influenced by facial height, between +1.54 and +1.64. A rough estimate of *temporalis* cross-sectional area scales from c. +1.4 to +1.9, indicating that the greater load of the allometrically lengthened lever arm is more than matched in larger species by the positive allometry of the power arm and of muscle cross-sectional area and so muscle force.

Larger species produce more bite force for their size than smaller ones due to the allometric changes in masticatory biomechanics following from increased body size, a point neatly illustrated by Demes et al., who demonstrate that skulls of *H. klossi* and *P. paniscus* enlarged isometrically to the size of *H.* (*S.*) *symphylangus* and *G. gorilla*, respectively, produce lesser bite forces than the "real" latter two forms do. Bite pressure (bite force/crown area) is maintained if bite force increases at the same rate as crown area; broadly similar relationships for these variables hold within hylobatids and great apes, indicating that in hominoids, crown area and bite force increase at about the same rate, at least over the size range of extant taxa. Estimated bite pressure is generally greater in great apes than hylobatids, although the orangutan is an exception here. Bite pressure shows no obvious relationship to between-species differences in size or diet; interestingly, *P. troglodytes* males produce the greatest scaled bite pressure, exceeding even *G. gorilla* males. Within species, males generally produce greater pressures than females, although whether this is selected for (implying differences in food processing or paramasticatory activity between the sexes) or is a by-product of selection for larger body size is a moot point. Demes et al. make the important point that similar allometric relationships obtaining within hylobatids and great apes provide strong evidence that biomechanical constraints associated with increased body size elicit similar functional responses across the Hominoidea. This is strong presumptive evidence that they should also be applicable to fossil forms.

Ravosa (2000) undertook such a combined allometric analysis of mandible size and form in fossil and extant apes, comparing them with cercopithecoids. Deeper corpora counter parasagittal bending while the more robust cross sections of larger species, especially the fossils, counter axial torsion. The positive allometry of corpus and symphysis cross sections suggests increased masticatory stresses due to greater balancing side muscle activity during powerful mastication, probably reflecting a tougher, harder diet. In addition, the allometry of jaw length and breadth point to greater wishboning stresses at the symphysis at the end of the masticatory powerstroke, countered by a thicker symphysis and increased anterior jaw breadth. After allometric scaling, the most robust mandibles include *Proconsul africanus* and *P. nyanzae*, *Rangwapithecus*, *Turkanapithecus*, *Afropithecus*, *Ankarapithecus*, *Lufengpithecus*, and *Ouranopithecus*; the more slender include hylobatids, *Simiolus*, *Hispanopithecus laietanus*, *Pan paniscus*, and *P. troglodytes* (see also below).

In the broader context of fossil (as well as extant) hominoids, even *G. gorilla* has a comparatively low and slender corpus, only average symphyseal height and a slightly broader than expected symphysis for its mandible length. *Pongo* has a higher but rather thinner corpus than expected and a higher symphysis of expected width; *P. paniscus* has a corpus and symphysis of expected height but rather thinner than expected, while *P. troglodytes* has a shallower, narrower corpus and symphysis, although the latter is closer to the values expected on jaw length than the former. These findings have implications for the dietary reconstruction of fossil forms: many Middle/Later Miocene hominoids are notably more robust than modern apes and so are plausibly reconstructed as exploiting harder, more resistant food items requiring substantial force in processing, while the categorization of proconsulids as “frugivorous” may also well underplay the variety and toughness of their dietary items. Such reconstruction, however, is difficult to reconcile with the evidence provided by dental morphology and wear patterns in *Proconsul* and by some other aspects of jaw form (see below).

In some respects, hominoid and cercopithecoid mandibular cross-sectional scaling patterns are similar; smaller apes are notably gracile, resembling cercopithecine proportions, but larger ones have both deeper and relatively wider corpora more reminiscent of colobines to resist greater axial torsion during chewing – perhaps reflecting larger, more laterally placed masseters that contribute relatively more to unilateral mastication, together with the medial pterygoids. This is especially so in the largest apes which have absolutely and relatively very thick corpora exceeding colobine proportions, suggesting diets with at least comparable, and very possibly greater, physical properties of hardness and/or toughness.

Smaller apes also display symphyseal curvature comparable to cercopithecines, whereas, with increasing body size, curvature reduces to a shallower, colobine-like, arc, eventually falling below even that in the largest apes. This has traditionally been interpreted in dietary terms (frugivores requiring large incisors and so a wide anterior dental arcade), but the bulk of the fossil evidence points to diets other than frugivory. Ravosa (2000) therefore interprets the broader anterior dental arcade combined with a relatively thick symphysis as hominoid adaptations to resist concentrated wishboning forces at elevated levels resulting from a hard-object diet. The exception to this is *Afropithecus*, which has a notably narrow, tightly curved anterior mandible with, presumably, correspondingly concentrated wishboning forces, raising interesting issues about dietary composition and food processing activities in that genus. Again, findings from the dental evidence do not easily accord with those based on mandibular proportions.

More recently, Taylor (2002, 2003) has used morphometric methods to investigate masticatory variation in African apes as a function of dietary differences. She compared allometrically adjusted mandibular, cheek, and facial dimensions, quantifying masticatory parameters associated with bite force and load resistance in ontogenetic series of bonobo, chimpanzee, and gorilla, to test the hypothesis that more folivorous forms would show greater development of these features.

The results are complex. Unsurprisingly, all species show allometric increases during growth in traits indicating improved muscle and bite force and the capacity to resist greater loads. Masticatory muscle sizes are especially strongly allometric. After adjusting for allometry, however, only a few traits differ consistently across African ape species as predicted by dietary preferences. A more resistant diet is generally correlated with a thicker mandibular corpus, although the thicker corpus of chimpanzees compared with bonobos is not matched by evidence of corresponding dietary differences. Compared with *Pan*, *Gorilla* has a relatively wider mandibular corpus to resist axial torsion, a wider symphysis so resisting "wishboning," a higher temporomandibular joint which contributes to improved mechanical advantage of the jaw lever and distributes forces more evenly along the cheek teeth, and a higher mandibular ramus, increasing the moment arm of the temporal and masseter muscles and providing a larger attachment area for the latter and the medial pterygoids. Moreover, within *Gorilla*, eastern gorillas exhibit greater values than western ones and also have larger masseter muscle than the latter, in accord with their more resistant diet.

Other analyses, however, do not conform to the pattern predicted from diet; for example, gorillas do not have the relatively deeper corpora expected to resist parasagittal bending (Hylander 1979a, b), and there was no regular association of the deeper symphysis providing increased resistance to bending and shearing forces with greater folivory (see also Ravosa's findings summarized above, although Demes et al. (1984) and Wolff (1984) considered the torsional resistance of the gorilla mandible "remarkable," and maximal at the symphysis). Overall, gorillas do not have the shorter deeper faces and more anteriorly positioned masticatory muscles predicted to improve the mandible's power arm ratio and to reduce bending moments in the face, and there was no consistent differentiation of bonobos and chimpanzees. Taylor concludes that while some of the distinctive craniofacial features of the African apes can plausibly be considered as dietary adaptations, the link is not especially strong. Dental development and allometric and other ontogenetic constraints are doubtless important influences, while more information is needed on the composition, variability, and especially the physical properties of ape diets. The equivocal nature of these results accords with those from some other studies; for example, despite their dietary contrasts, Rak's indices quantifying relationships between the palate, masseter origin, and their positions relative to the calvaria fail to discriminate between *Pan* and *Gorilla* (Rak 1983: table 3, p 25).

Further analysis of the *Gorilla* masticatory system with larger samples, and including *G. g. graueri* in the analysis, confirms and extends the earlier findings (Taylor 2003). *G. g. beringei* has a significantly larger face than the other two subspecies and differs from *G. g. graueri* in the same features that distinguish it from *G. g. gorilla* and which differentiate *Gorilla* and *Pan*. Despite being more folivorous, however, *G. g. graueri* does not differ from *G. g. gorilla* in those features, and *G. g. beringei* fails to express the full set of masticatory traits predicted by its diet. In this last respect, it may well be the case that an investigative model assuming optimization of each and every variable is simply inappropriate; rather than a spectrum or continuum of values for every trait, some may be more appropriately considered in terms of thresholds. For example, if food availability is not a constraint and provided the face is structurally sufficiently strong to resist masticatory forces, there seems little reason to suppose that selection will necessarily promote further shortening and deepening of the face in hominoid folivores to achieve “optimal” values, particularly if to do so will disrupt pervasive, well-established allometric trajectories. Covariation within a tightly integrated functional system, such as the head, is likely to impose multiple constraints on the variation of any given character or character complex.

Taylor et al. (2008) report a detailed analysis of the relationships between jaw form, diet, and food properties in orangutans, chimpanzees, and gorillas, using area moments of inertia and condylar area ratios to estimate moments imposed on the mandible to assess relative ability to counter mandibular loads. They took data on elastic modulus and fracture toughness of food types to derive food material properties and generated bending and twisting moments on the mandible to estimate minimally required bite forces. Based on food properties, they hypothesized improved resistance to mandibular loads in *Pongo p. wurmbeii* compared to African apes and in *Gorilla b. beringei* compared to *Pan t. schweinfurthii*. The predictions were, in fact, only applicable when bite forces were estimated from maximum fracture toughness of non-fruit, non-leaf vegetation; for all other tissues (fruit, leaves) and material properties, results were contrary to predictions. As food material properties changed, moments imposed on the mandible changed, so altering ratios of relative load resistance to moment, so that species appear over- or under-designed for the moments imposed on the mandible. Reliable estimates of average and maximum bite forces from food material properties accordingly require information about the physical properties of the full range of dietary items.

A recent study (Taylor and Vinyard 2013) incorporates data on masticatory muscle physiologic cross-sectional area (PCSA) and muscle fiber length and broadly confirms an allometric influence on masticatory power while underlining the need for caution when inferring chewing forces from skull form. Hominoid muscle fiber architecture reflects both absolute size and allometric influences; PCSA is close to isometry relative to jaw length in anthropoids but trends to positive allometry in hominoids. Extant large-bodied apes therefore probably generate absolutely and relatively greater muscle forces compared with hylobatids and monkeys, possibly reflecting changes in food composition, ingestive behavior, and/or increased emphasis on mastication as opposed to ingestion with greater body size. The study also revealed that craniometric estimates of masseter and temporalis PCSA may be seriously awry, underestimating the actual figures by >50 % in gorillas and overestimating masseter PCSA by up to 30 % in humans.

Given the lack of concordance in masticatory morphology and diet in living hominoids, and the discongruities between craniofacial morphology and dental evidence among fossil forms, detailed dietary reconstruction based on craniofacial form in fossil hominoids appears questionable. There seems no secure basis on which to go beyond the most general of statements about dietary properties. Shea's conclusions about the relative decoupling of masticatory morphology and diet in the African apes may be applicable to hominoids generally (see also Daegling and Hylander (1998, 2000) and Daegling (2004)). Dental evidence (crown proportions and morphology, crest development and structure, chemical composition, and wear patterns) may well prove a better guide to hominoid diets than the analysis of craniofacial form, no matter how elaborate the biomechanical models employed (Ungar 1998; Teaford and Ungar 2000). These provisos should be kept in mind in relation to the following summary of craniofacial form in fossil hominoids, which for its framework draws especially on the chapters by Harrison, Begun, Kelley, and Ward and Duren in Hartwig (2002).

Fossil Hominoids

Africa

Oligocene/Early Miocene African Hominoids

The splitting event between the two crown groups of the Catarrhini, apes and Old World monkeys, was an African phenomenon, as the earliest members of both lineages are found in sub-Saharan Africa. The earliest evidence for the divergence is known from late Oligocene (25.2 Ma) deposits in the Rukwa Rift Basin in southwestern Tanzania; *Nsungwepithecus gunnelli* shows evidence of bilophodont, a cercopithecoid synapomorphy, while *Rukwapithecus fleaglei*, from the same deposits, shares two dental traits with crown hominoids – M_2 hypoconulid positioned buccally and a hypoconid positioned opposite the lingual notch between the metaconid and the entoconid (Stevens et al. 2013). The dental similarities of the latter taxon with *Rangwapithecus* from the early Miocene of Kenya may suggest a similar dietary adaptation, namely, folivory (see below).

Kamoyapithecus

The other known late Oligocene catarrhine that has been considered a possible hominoid is *Kamoyapithecus*, from Lothidok, Kenya (Leakey et al. 1995). No explicit shared derived traits link the form with later hominoids. Although very little can be said about the maxillary bone preserved in the type specimen, the dentition is consistent with a high degree of anterior tooth use, albeit with thinner dental enamel than that seen in later, similarly sized forms, such as *Afropithecus*.

More extensive evidence from Early Miocene sites in East Africa indicates an array of forms, variously regarded as hominoid or non-hominoid (see chapter "▶ Fossil Record of Miocene Hominoids," Vol. 2). Evidence from the oldest (19–20 Mya) sites of Songhor and Koru (Kenya) points to predominantly tropical forest habitats, with later (16–17 Mya) sites on Rusinga Island (Kenya) ranging from flood plain to riverine contexts. The picture here is of drier, more seasonal environments than Songhor or Koru, but with persistent wooded conditions, varying from forest to deciduous woodland according to rainfall (Andrews 1996; Andrews et al. 1997). Similar habitats are indicated at the rather later Middle Miocene sites of Maboko Island (15–16 Mya) and Fort Ternan (14.5 Mya; see below).

Micropithecus

The small (ca. 3.5 kg) *Micropithecus* contrasts the bulk of the Early Miocene non-cercopithecoid fauna dentally in having relatively larger anterior teeth compared to the cheek teeth, broad incisors, and narrow premolars and molars, with only weakly developed occlusal ridges. It differs cranially from the similarly sized *Dendropithecus* in its shallow, broader palate and nasal aperture, short face and clivus, and moderately high and lightly built mandible corpus, with only modest symphyseal tori. Phylogenetic analyses (Rae 1993, 1997; Stevens et al. 2013) suggest that this taxon may be a stem hominoid, as it lacks some of the characteristic hominoid cranial synapomorphies. The frequency of dental pitting and pit shape in *Micropithecus clarki* (19–20 Mya) points to folivory (Ungar et al. 2004), while *M. leakeyorum* (15–16 Mya) shows similarities to the rather earlier *Simiolus enjessi* (16.5–18 Mya) that probably also reflect folivorous adaptations (Harrison 1989; Benefit 1991).

Proconsul

At least two broad cranial morphologies are represented among the Lower Miocene fossils. The genus *Proconsul* is particularly well known, with species differing in size and dental and gnathic details, but linked by fundamental similarities in craniodental morphology (Fig. 7). Knowledge of *Proconsul* is primarily based on the material recovered from sites on Rusinga Island, Kenya, including much of a skull in 1948 (Le Gros Clark and Leakey 1951) and a partial skeleton from 1951 and subsequently (Napier and Davis 1959; Walker and Teaford 1989; Walker et al. 1993) supplemented by other material. Initially assigned to the type species *P. africanus*, the 1948 and 1951 specimens were later transferred to *P. heseloni* (Walker et al. 1993; Walker 1997) on the basis of differences in dental size and morphology and in mandibular proportions and symphyseal reinforcement from the type of *P. africanus* from Koru.

Fig. 7 (*Upper*) Frontal and profile views of *Proconsul heseloni* cranium (Photograph © National Museums of Kenya). (*Lower*) Frontal and profile views of *Proconsul nyanzae* part face (Photograph © National Museums of Kenya)

Compared with later hominoids, the *P. heseloni* cranium is lightly constructed: the globular neurocranium largely lacks pronounced tori or crests, although the medial portion of the nuchal crest is evident above the steeply angled nuchal area, and the external occipital protuberance is located high on the skull rear. The frontal is short but broad, reflecting the limited postorbital constriction, while the superior temporal lines are prominent anteriorly and converge toward the vault rear but do not meet to form a crest. On the face, the premaxilla rises on either side of the nasal aperture, contacting the nasal bones above their tip, so excluding the maxilla from the rim of the nasal aperture, which narrows inferiorly between the central incisor roots above a short nasoalveolar clivus. Above it, the nasal bones are nonprojecting, long, and narrow, extending upward beyond the frontomaxillary suture and expanding in breadth in the glabellar region. There is a prominent jugum above the upper canine root and a shallow canine fossa. The lightly built zygomatic arch originates low down, curving backward and upward, and has a well-developed malar tuberosity. The subrectangular orbits are widely separated, surmounted by weak supraorbital ridges and with a slightly swollen glabella over a large frontal sinus (which may represent a frontoethmoid sinus; see Rossie 2005) between, but there is no distinct supraorbital torus.

The palate is long, rectangular, and shallow. A large, transversely broad incisive fossa joins directly with the nasal cavity, so there is no true incisive canal, and the hard palate is retracted from the subnasal alveolar process (Ward and Pilbeam 1983; McCollum and Ward 1997). There is a pronounced tuberosity on the alveolar process behind M^3. The maxillary sinus extends anteriorly to the premolars and laterally into the root of the zygomatic arch. The articular eminence and postglenoid process are well developed, and the auditory region has a tubular ectotympanic as in modern catarrhines, while the prominent, well-pneumatized mastoid process is coronally narrow and rather bladelike.

The mandibular symphysis exhibits a moderately to well-developed superior transverse torus but a much weaker and variable inferior torus, absent altogether in some individuals. The corpus displays limited lateral buttressing below the cheek teeth and shallows posteriorly; the relatively high ramus is lightly constructed, and the gonial region only slightly marked by muscle attachments. The slightly earlier, similarly sized and evidently closely related *P. africanus* differs from *P. heseloni* in numerous dental details, mandibular proportions, and symphyseal reinforcement: the *P. africanus* corpus is deeper anteriorly and posteriorly shallows more strongly, while the symphysis lacks an inferior transverse torus but bears a pronounced superior torus (Walker et al. 1993). An inferior transverse torus is also absent in the larger *P. nyanzae*.

Views differ on *Proconsul's* brain size and encephalization: Walker et al. estimated the 1948 cranium's capacity as 167 cm^3 and inferred that *P. heseloni* was more encephalized than modern cercopithecoids of similar size. Manser and Harrison (1999), however, using foramen magnum area as a size surrogate, estimated brain size as the markedly lower 130 cm^3 and close to the mean encephalization value for anthropoids. The endocast's relatively small frontal lobe and cortical sulcal pattern were considered primitive and cercopithecoid by Le Gros Clark and Leakey (1951) and Le Gros Clark (1962) but definitely not so by Radinsky (1974) who judged it hominoid and most like gibbons. More recently, Falk (1983) has argued that the sulcal pattern resembles that of extant New World monkeys, such as *Ateles*, rather than any group of catarrhines and approximates the inferred common ancestral sulcal pattern for Anthropoidea.

Relative shearing-crest lengths in those *Proconsul* species studied (*P. heseloni*, *P. nyanzae*, and *P. major*, the last sometimes referred to the genus *Ugandapithecus*; see below) are less than those of any extant ape and considered to indicate frugivory (Kay and Ungar 1997), while the proportion of pits to scratches on molar wear facets (37–39 %) also indicates soft-fruit eating (Ungar 1998; Ungar et al. 2004). Despite the findings of Ravosa (2000), see above, mandibular form and proportions are also compatible with this interpretation. At the symphysis, the prominent superior transverse torus and minimal or absent inferior torus produce a broadly triangular cross section, especially in larger individuals, resistant to torsional or bending stresses produced by medial (jaw opening) or lateral (masticatory power stroke) bending (Hylander 1984; Brown 1997). Below the cheek teeth, the corpus is relatively deep vertically and narrow coronally, and, while it may be reinforced by the rear of the superior transverse torus, the mylohyoid ridge, and the lateral eminence, there is relatively little change in cross-sectional shape along the corpus compared with other fossil apes (Brown 1997). This suggests chewing activity generating comparatively high vertical forces but only limited transverse or torsional forces during food processing.

It is also possible to infer aspects of the locomotor pattern of fossil taxa with reference to their cranial morphology via the semicircular canals of the middle ear; there is a general correlation between the radius of curvature of the organ of balance and the relative agility of primate taxa (Ryan et al. 2012). The ancestral catarrhine adaptation, judged from stem forms such as *Aegyptopithecus*, is that of a

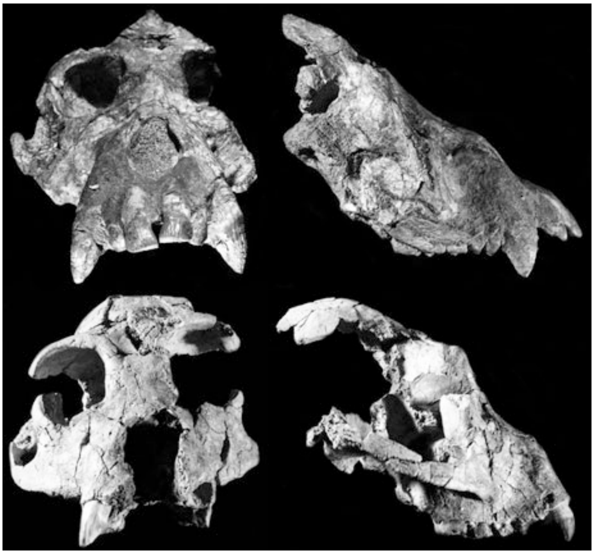

Fig. 8 (*Upper*) Frontal and profile views of *Afropithecus turkanensis* cranium (Photograph © National Museums of Kenya). (*Lower*) Frontal and profile views of *Turkanapithecus kalakolensis* cranium (Photograph © National Museums of Kenya)

medium-slow arboreal quadruped. *P. heseloni*, however, is characterized by larger semicircular canals, which suggests more agile, medium-speed locomotion, much like that seen in extant macaques.

One species previously assigned to *Proconsul* is now considered by some to be distinct at the generic level (Senut et al. 2000); *Ugandapithecus* is held to contain as many as four species of varying sizes and chronological ages (Pickford et al. 2009b), including the only-just-named *Proconsul meswae* (Harrison and Andrews 2009). The largest (and least contentious) of the species, *U. major* from Songhor in Kenya and Napak in Uganda, has little in the way of cranial material preserved, although all of the taxa assigned to *Ugandapithecus* are said to share a distinctive mandibular corpus that becomes shallower posteriorly. It is worth noting, however, that the generic distinction is not recognized universally (MacLatchy and Rossie 2005).

Afropithecus

The contemporary *Afropithecus turkanensis* contrasts markedly with *Proconsul* in its cranial form (Leakey and Walker 1997) (Fig. 8). The large face is dominated by the long domed muzzle and deep, flaring zygomatic processes. The projecting premaxilla forms a deep nasoalveolar clivus and extends up on both sides of the broad, oval nasal aperture to contact the narrow, medially elevated nasal bones. There is an extensive maxillary sinus; the shallow palate displays large paired openings for the incisive foramen. The canine roots form prominent juga; the root of the zygomatic process is deep, anteriorly inferiorly sloping, and originates low down on the face. The cordiform orbits are broader than high, inferolaterally sloping and widely separated. The glabellar region is prominent, the slender supraorbital torus curving above each orbit and delimiting a frontal trigon with its lateral limits marked by well-defined anterior temporal lines which merge to form a distinct sagittal crest. Postorbital constriction is marked, and the *temporalis* muscles are well developed. The mandibular corpus is very deep with a distinct fossa, while the ascending ramus is set obliquely to the corpus. The symphysis bears moderate superior and inferior transverse tori, a long and strongly sloping subincisive planum, and a low-genial pit, implying a deep, narrow tongue.

Overall facial proportions of *Afropithecus* are reminiscent of *A. zeuxis*, but absolutely much larger; finite element scaling analysis reveals marked size contrasts but minimal shape differences in the snout and some shape differences (but reduced size contrasts) in the zygomatic and maxillary tuberosity regions (Leakey et al. 1991). These authors conclude that the similarities in *Aegyptopithecus* and *Afropithecus* facial form indicate the persistence into the Early Miocene of a functionally integrated mosaic of features that characterized the primitive hominoid face. Benefit and McCrossin (1991) draw attention to craniofacial similarities between *Aegyptopithecus*, *Afropithecus*, and the Miocene cercopithecoid *Victoriapithecus*, indicating that many of these facial traits are primitive catarrhine characters rather than basal hominoid synapomorphies.

With its large, procumbent, and mesially inclined upper central incisors; stout, low-crowned canines; and cheek teeth covered with very thick enamel and complex wrinkling, *Afropithecus* has been compared, especially in its anterior dentition, to pithecines exploiting seeds and hard fruits, where the incisors crop food items and the large canines apply considerable force to puncture hard fruits, as in *Chiropotes* (Leakey and Walker 1997; Kinzey 1992). Cusp morphology, the high incidence of pitting in the single *Afropithecus* individual sampled – at 43 %, the highest of the early African forms studied (Ungar et al. 2004) – and a lack of prominent shearing crests on the cheek teeth are also consistent, like the anterior dentition, with frugivory.

Overall, Leakey and Walker (1997) conclude that *Afropithecus* was a sclerocarp forager. Other aspects of mandible reinforcement (e.g., strong basal buttressing, a pronounced lateral tubercle where the oblique line meets the corpus, a hollowed buccal surface above the mental foramen with a marked canine jugum anteriorly) that support this interpretation are also seen in *Sivapithecus* (see below) and probably reflect comparable biomechanical responses to reliance on food items with similar physical properties rather than any especially close phylogenetic link. The somewhat smaller but otherwise similar *Heliopithecus* from the early Middle Miocene of Saudi Arabia may be no more than specifically distinct from *Afropithecus* (Andrews et al. 1978; Andrews and Martin 1987).

Morotopithecus

The large (chimpanzee-sized) hominoid *Morotopithecus bishopi* (Gebo et al. 1997), based on the palate from Moroto initially assigned to *P. major* (Pilbeam 1969), resembles *Afropithecus* in many respects and may be congeneric with it. It is of

Early (20–21 Mya) or Middle (15–17 Mya) Miocene age, depending on ^{40}Ar^{39}/Ar dating (Gebo et al. 1997) or faunal correlation (Pickford et al. 1999). It combines an anteriorly broad palate with comparatively narrow, procumbent incisors offset by a pronounced diastema from the large, stout canines, whose massive roots form pronounced juga. The molars resemble those of *P. major* in their bunodont cusps, wrinkled enamel, and beaded lingual cingulum, but contrast in their relative sizes, while the anterior dentition is much larger and the interobital breadth narrower than in *P. major*. Overall the face is relatively long and narrow, with a broad nasal aperture, a short clivus, and an extensive maxillary sinus. The undoubted resemblances in face and dentition to *Afropithecus* may reflect dietary convergence in exploiting hard-cased fruits rather than phylogenetic propinquity. Postcrania referred to *Morotopithecus* resemble those of *Proconsul* in some respects but are also markedly more derived in the direction of modern hominoids in the lumbar, shoulder, hip, femur, and knee regions and point to forelimb suspension and slow brachiation, as well as climbing and quadrupedal activity in an arboreal habitat (MacLatchy 2004).

Nyanzapithecus

Nyanzapithecus is much less well known, but premaxillary and maxillary fragments of two species, *N. vancouveringorum* from the Early Miocene (17–18.5 Mya) and *N. pickfordi* from the Middle Miocene (15–16 Mya), indicate contrasts with *Afropithecus* in their smaller size; shorter faces; low, broad nasal apertures; and robust premaxillary regions (Harrison 2002). These species and the rather smaller Middle Miocene *N. harrisoni* (13–15 Mya) display broad, strongly built upper and lower incisors, while the cheek teeth are long and narrow; the molars bear low, expanded cusps and rounded occlusal crests. *Mabokopithecus*, represented by two isolated rear lower molars and an almost complete mandible, is dentally very similar to *N. pickfordi* and may well be congeneric with *Nyanzapithecus*, in which case the former genus has priority.

Rangwapithecus

The Early Miocene (19–20 Ma) *Rangwapithecus gordoni*, similar in size and probable locomotor pattern to the smaller *Proconsul* species, contrasts dentally with them in numerous respects, including molars with low cusps and well-developed crests, enamel wrinkling, and a pronounced wear differential. Cranial material indicates a comparatively short premaxilla and long, narrow palate widening toward the rear. The maxillary sinus is deep and the zygomatic root set low down the face above M^1–M^2; the mandible is deep and the symphysis reinforced with a pronounced superior transverse torus. Kay and Ungar (1997) and Ungar et al. (2004) have argued that, on the basis of its molar crest development (greater than that of any other Early Miocene form) and the low incidence and long, narrow form of dental pitting, *Rangwapithecus* is likely to have been folivorous. Dental proportions and macrowear, facial morphology, palatal proportions, and mandible structure are all compatible with this interpretation.

Turkanapithecus

The somewhat younger (16.6–17.7 Mya) *Turkanapithecus kalakolensis* is another medium-sized form, rather smaller than *P. heseloni*, and represented by a partial cranium preserving the upper dentition save for the incisors and a mandible with left M_2 and right M_3 (Fig. 8). The skull exhibits a relatively short face with broad, domed snout; a wide, oval nasal aperture flanked by prominent canine pillars, with expanded nasal bones; and a broad, flat interorbital region above. The palate is narrow, with posteriorly convergent tooth rows, and there is an extensive maxillary sinus. The zygomatic process originates low down on the face, and the arch is relatively deep and flaring. This, combined with pronounced postorbital constriction, makes for a deep infratemporal fossa and, presumably, well-developed *temporalis* muscle – a view also supported by the strongly marked and convergent temporal lines, pointing to a sagittal crest. The rear of the saddle-shaped glenoid cavity is bounded by a well-developed postglenoid process, but there is no distinct articular eminence. The nuchal area is comparatively short and the crest strongly developed, reflecting both the rugged facial architecture and comparatively small neurocranium, estimated at c. 85 cm^3 – absolutely and relatively smaller than *P. heseloni* (Manser and Harrison 1999).

Given this cranial morphology, it is rather surprising that the mandibular symphysis displays neither strongly developed superior nor inferior transverse tori. The corpus is shallow and relatively slender, with constant depth below the molars, while the ramus is broad, low, and sloping, with an expanded gonial region, so according with zygomatic architecture indicating well-developed masseter muscles – and a knoblike condyle. Upper first premolars are large, and while both upper and lower molar teeth increase in size posteriorly, the gradient is much less than in comparably sized *Proconsul* species. Overall, craniodental features suggest a resistant diet, possibly consisting of hard-cased fruits or leaves.

Dendropithecus

There is also a cluster of small- to medium-sized forms (perhaps 3–9 kg), usually grouped together as dendropithecoids. The siamang-sized *Dendropithecus macinnesi*, based on material originally assigned to *Limnopithecus*, displays narrow, high-crowned incisors; strongly dimorphic canines; broad premolars; and molars with high cusps, sharp occlusal crests, and well-defined foveae. The palate is narrow, as is the nasal aperture; the maxillary sinus is extensive and the mandible corpus low and robust, with the symphysis reinforced by fairly prominent superior and inferior transverse tori. Among Early Miocene hominoids, *Dendropithecus* has the least well-developed molar shearing crests of those studied other than *Proconsul* and a fairly high incidence of pitting, pointing to a predominantly soft-fruited dietary niche (Kay and Ungar 1997; Ungar et al. 2004).

Limnopithecus

Other small Early Miocene forms, known principally from isolated teeth and part jaws, include *Limnopithecus legetet* and *L. evansi*. These have a short lower face, with anteriorly positioned orbits; narrow, elliptical nasal aperture; and a shallow clivus, an inflated maxillary sinus, and a shallow, lightly built mandible reinforced symphyseally by a strongly developed superior transverse torus but with an inferior torus that is weak (*L. evansi*) or absent (*L. legetet*). *L. legetet* combines broad, low-crowned incisors and small canines with an ovoid P_3 that suggests only part development of the C–P_3 honing complex, and cheek teeth with high, sharp cusps and occlusal crests. *L. evansi* has narrower, higher crowned incisors, larger canines, and a better developed sectorial face on P_3, cheek teeth with lower, rounded cusps, and less sharply developed occlusal crests. Relative shearing-crest development suggests a fairly folivorous niche (Kay and Ungar 1997).

Kalepithecus

Less well known than these forms is the broadly contemporary *Kalepithecus songhorensis*, similar in dental size to *L. legetet*, but differing in most other respects. The anterior teeth are relatively large, with I^1 broader and more spatulate, the upper premolars relatively narrow but the molars relatively broad; P_3 is moderately sectorial, the short, broad lower molars with low, rounded, and expanded cusps, and poorly developed occlusal crests. *Kalepithecus* contrasts with other Early Miocene forms in its inferiorly broad nasal aperture and deep clivus, while dental morphology and proportions suggest a frugivorous diet.

Middle and Late Miocene African Hominoids

Fossil hominins apart, evidence of African hominoids from the Middle Miocene onward is limited, especially, when contrasted with the comparatively abundant Early Miocene material. Nonetheless, recent discoveries have both significantly increased the number of fossils (Ward and Duren 2002) and led to major reappraisals of earlier finds, notably of the material assigned to "*Kenyapithecus*" *africanus* (Leakey 1967), which has been reallocated to distinct taxa, with consequent systematic and phyletic implications.

Nacholapithecus

One such taxon is the large, markedly dimorphic *Nacholapithecus kerioi* (Ishida et al. 1999, 2004), based on material from Middle Miocene (15 Mya) sites in Samburu District, Kenya. Cranial remains display overlap of the posterior premaxilla and hard palate, forming a short incisive canal (Kunimatsu et al. 2004), which may indicate an intermediate condition between the nonoverlapping subnasal configuration of gibbons and fossil stem hominoids and the longer incisive canal that is a diagnostic trait of the clade that includes the extant large-bodied apes (Nakatsukasa and Kunimatsu 2009), or Hominidae. The incisive foramen is small, while the face bears strong canine pillars and deep fossae, and the zygomatic process originates low down on the maxilla. The mandible corpus is tall but thin, with a near vertical symphysis, a moderate inferior transverse torus, and a lateral fossa below the premolars. I^1 is high crowned and robust, while both lower incisors are tall and narrow. Canines are low crowned, upper premolars display marked cusp heteromorphy, and molars are thick enameled.

Equatorius

Other material previously assigned to "*K.*" *africanus* has been incorporated, along with new discoveries (including a part skeleton (KNM-TH 28860) from Kipsaramon, Tugen Hills, and multiple finds at Maboko Island and adjacent localities, Kenya), in another, broadly contemporary (14–15.5 Mya) large-bodied, dimorphic species *Equatorius africanus* (Ward et al. 1999). While initially criticized – see, for example, Begun (2000) and Benefit and McCrossin (2000) and response by Kelley et al. (2000) – the current consensus is that *E. africanus* is a valid taxon. The species is characterized by broad I^1s with marginal ridges, markedly asymmetrical lateral incisors, with a spiral lingual cingulum, and relatively large upper premolars with reduced cusp heteromorphy (contra *Nacholapithecus*). The procumbent, narrow lower incisors are tall, whereas the mandibular canines are low crowned with convergent roots. The thick-enameled, bunodont lower molars increase markedly in size along the tooth row.

The maxilla exhibits a very low, broad root for the zygomatic process and an extensive sinus extending into the premolar region, while the mandible displays a long, inclined sublingual planum, a prominent inferior transverse torus, and a robust corpus. The partial skeleton and other postcranial fossils indicate some resemblances to earlier forms such as *Proconsul* and *Afropithecus*, but with forelimb and hind limb contrasts that point to significant terrestriality (Sherwood et al. 2002; Patel et al. 2009). It remains to be determined whether ground vegetation formed an appreciable component of *Equatorius*' diet, but dental similarities to *Afropithecus* (and "*Heliopithecus*"), especially in canine form and premolar proportions, suggest resistant foods, such as seeds and/or hard-cased fruits, as major dietary items.

Kenyapithecus

The genus *Kenyapithecus* is retained for the rather later (14 Mya) species *K. wickeri*, known from partial jaws and isolated teeth from Ft. Ternan, Kenya. The maxilla exhibits marked canine fossae, a relatively low and anteriorly positioned origin for the zygomatic process above M^1, little extension of the maxillary sinus into the inflated alveolar process (in contrast to *Equatorius*), and a relatively highly arched palate. The upper incisors are markedly heteromorphic, with I^2 much smaller than I^1, which is reinforced by strong lingual marginal ridges extending across the base of the crown surface. The upper canines exhibit marked dimorphism: robust, tall, and externally rotated in presumed males, more conical in females. P^4 is relatively broad with subequal cusps; M^1 is quadritubercular and lacks a lingual cingulum, while M^2 is similar but larger. The postcanine teeth are closely packed, with low cusp relief and appreciable wear.

The mandible, considered female, displays a shallow symphysis, sharply retreating at 30–40° to the alveolar margin, with pronounced inferior transverse torus extending to below the mesial root of M_1, rather weak superior torus and long sublingual planum, a short incisor row, and a robust, comparatively shallow but thick corpus. As reconstructed, the mid-lower face overall was broad and flat, with wide cheeks and a short snout (Andrews 1971; Walker and Andrews 1973). The relatively tall-crowned lower canine bears only a slight lingual cingulum, while P_3 is obliquely set and sectorial, with a distinct honing facet for the upper canine, and P_4 bears prominent mesial and smaller, lower distal cusps; the poorly known lower molars apparently lack buccal cingula.

The narrow anterior dental arcade, procumbent incisors with curved roots, anteriorly positioned zygomatic origin, restricted maxillary sinus and mandible with markedly sloping symphysis, pronounced inferior transverse torus, and shallow, robust corpus differentiate *K. wickeri* from most other African hominoids. Andrews (1971) and Walker and Andrews (1973) interpret these traits as a functional set adapted for powerful chewing activity with a strong lateral grinding component and pronounced incisal action. There are similarities, especially in the anterior dentition, with *Afropithecus*, and, as with that genus, pithecines have been proposed as the most plausible dietary analogues (Leakey and Walker 1997; McCrossin and Benefit 1997). This model of *K. wickeri* as a sclerocarp feeder, exploiting hard-cased/hard-stoned fruits, seeds, and nuts, is compatible with reconstruction of the Ft. Ternan environment as drier and more seasonal than many earlier African sites, predominantly closed-canopy woodland with both open country and forested conditions nearby (Andrews 1996; Andrews et al. 1997). A second species of this genus, *K. kizili* (Kelley et al. 2008), has been named for material found outside of Africa and will be treated below.

Otavipithecus

Broadly contemporary at 13 + 1 Mya, the more southerly *Otavipithecus namibiensis* is known from a part mandible and frontal bone from Berg Aukas, Namibia (Conroy 1997; Conroy et al. 1992). The incisor region of the mandible is narrow and the symphysis reinforced by a short inferior transverse torus. The corpus is robust, of constant depth, and relatively long, with the ramus originating behind M3 and with a distinct retromolar space. Premolar and molar cusps are inflated and bunodont, mesial, and distal foveae small and enamel thin. The frontal bears superciliary ridges rather than a transverse torus, with marked temporal ridges adjacent to glabella, relatively wide interorbital dimensions and an extensive frontal sinus. The last of these traits has been used to link *Otavipithecus* with extant hominines (Pickford et al. 1997), but the current lack of clarity as to the polarity of frontal sinus evolution in catarrhines renders this interpretation premature at best. The narrow incisor region does not support a niche of specialized frugivory, while the thin enamel and minimal wear differential on the molar teeth point to a nonabrasive diet; there are no obvious dental adaptations to folivory. Conroy argues that *O. namibiensis* probably subsisted on a range of plant foods that required little preparation by the anterior teeth prior to chewing.

Samburupithecus

A later Miocene (9.5 Mya) large-bodied species from the Samburu Hills of north central Kenya named *Samburupithecus kiptalami* is known only from one left maxilla with P^3–M^3 crowns and the canine alveolus (Ishida and Pickford 1997). The palate displays a marked arch, a shallow postcanine fossa, a low origin for the zygomatic root, and invasion of the zygomatic process by the extensive maxillary sinus. The nasal floor has a sharp margin, and the tooth row is straight from the canine alveolus to M3. The three-rooted premolars have elongated crowns with coequal main cusps, while the molars display inflated, bunodont cusps and thick enamel. *S. kiptalami*'s affinities are unknown; some workers consider it to show some similarities with the gorilla, although there are also undoubted differences, e. g., the size of lingual cingulae. This and other traits make it most likely that *Samburupithecus* is a late-surviving part of the stem hominoid radiation that included *Proconsul* (Olejniczak et al. 2009).

Two newly discovered taxa have increased our knowledge of the later Miocene of Africa substantially. *Nakalipithecus nakayamai* is a large ape (>50 kg) from the early Late Miocene (9.9–9.8 Mya) site of Nakali, Kenya (Kunimatsu et al. 2007). Although known from only a few dentognathic remains, its striking resemblance to the slightly younger *Ouranopithecus* from Greece suggests that the popular paleobiogeographic scenario of large-bodied apes originating in Eurasia before reinvading Africa (Stewart and Disotell 1998) may need to be reexamined. The mandible of the holotype has a well-developed simian shelf (inferior transverse torus) and the thick dental enamel, reduced molar cingulae and reduced upper premolar cusp heteromorphy seen in Eurasian forms that have been considered more closely related to living hominids than African forms, although it retains the primitive non-compressed lower mesial premolar shape. A second large-bodied form, *Chororapithecus* is known from dental remains found in 10–10.5 Mya deposits in the Afar region of Ethiopia (Suwa et al. 2007). Aside from their similar size, the *Chororapithecus* molars are also similar to those of *Gorilla* in their relative development of molar shearing crests associated with folivory. Although not linked directly with the extant taxon, partly due to its thicker enamel caps, the resemblance suggests to the describers that it may belong to same clade. Two other possible new taxa, *Kogolepithecus* from the ca. 17 Mya site of Moroto II in Uganda (Pickford et al. 2003), and a single mandibular fragment from between 11 and 5 Mya in Niger (Pickford et al. 2009a) are too fragmentary to allow any convincing analysis.

Other, later taxa, closer to the Mio-Pliocene boundary (*Sahelanthropus*, *Orrorin*), are as yet only incompletely described but are claimed as basal hominins (see Senut, chapter "▶ The Miocene Hominoids and the Earliest Putative Hominids," Vol. 3). The known time span of *Pan* has recently been extended by the recovery of four fossil teeth (r and l I^1, l M^1, r M^3) from Middle Pleistocene deposits of the Kapthurin Formation of the Tugen Hills, Kenya, within the eastern Rift (McBrearty and Jablonski 2005). The broad, spatulate incisors bear deep mesial and distal foveae separated by a prominent lingual tubercle and the molars are low crowned, while all teeth exhibit thin enamel. The large hypocone on M^1 suggests *P. troglodytes* rather than *P. paniscus*, although McBrearty and Jablonksi are cautious in attributing specific identity, preferring assignment to *Pan* sp. indet. The finds date from around 0.5+ Mya, and the site lies some 600 km east of the present chimpanzee range. The teeth were discovered close to localities yielding part mandibles of *Homo* (*H. erectus* or *H. heidelbergensis*/*H. rhodesiensis*) pointing to sympatry and suggesting that adaptive scenarios which reconstruct differentiation of chimpanzee and hominin populations through the Rift Valley acting as an isolating barrier are unlikely to be correct. Fossil evidence for bonobos and gorillas is entirely lacking.

Europe and Asia Minor

While there is limited evidence dating from 15 to 17 Mya, the bulk of the European and west Asian hominoid material is from later Miocene sites between 6 and 12 Mya (Kay and Simons 1983; Pilbeam 2002). Many of these suggest subtropical seasonal forest or woodland as the dominant habitat; there is evidence of swamp conditions at some sites, while possibly harsher, more open environments are indicated at sites in Greece and Turkey yielding *Ouranopithecus* and *Ankarapithecus*, respectively.

Griphopithecus

The earliest evidence (13.5–17 Mya) consists of several low-crowned, large-cusped, and thick-enameled molars from Germany, Austria, and Slovakia assigned to *Griphopithecus*, a genus better known from Turkey, where a mandible with cheek teeth from Çandır and maxillary teeth from Paşalar dating from c. 15 Mya are referred to *G. alpani* (Alpagut et al. 1990). Like their European counterparts, the lower molars have bunodont, thick-enameled cusps, and well-developed buccal cingula. The upper central incisors are relatively narrow with a distinct median lingual pillar, and the male canines, especially in the upper jaw, are robust and comparatively low crowned. The mandible is strongly constructed, with both a prominent superior and well-developed inferior transverse torus at the symphysis and a long, shallowly inclined planum alveolare.

Heizmann and Begun (2001) suggest that *Griphopithecus* evolved from an *Afropithecus*/*Heliopithecus*-like thick-enameled ancestor and that this feature, together with the associated trait of low-dentine penetrance, was crucial to the expansion and success of dentally modern hominoids in the more seasonal Middle and Late Miocene habitats of Eurasia. However, at least one successful European form – *Dryopithecus* – had comparatively thin enamel, pointing to this as either a secondarily derived trait evolved from a thicker-enameled European ancestor or that the genus represents a second hominoid radiation into Europe.

Also at Paşalar, the species *Kenyapithecus kizili* (Kelley et al. 2008) is found. It has been linked to the African genus primarily due to the lack of lingual pillars in the upper central incisors, by which it differs from the other Paşalar hominoid *Griphopithecus*, although there are also some maxillary similarities. Unusually, the entire hypodigm of the taxon is thought to be from a single birth cohort, as all are the same developmental age and show identical enamel hypoplasias (Kelley 2008). As the molar teeth are extremely similar to those of *Griphopithecus*, it is assumed that their adaptation was similar, as well.

Dryopithecus

The thin molar enamel of *Dryopithecus* results in frequent dentine exposure, especially on the cusps, which lie close to the crown margins around a broad, shallow fovea. Below the narrow, low P_3 crown enamel extends onto the anterior root, pointing to at least partial honing against the upper canine (Begun 2002), while the upper central incisors are narrow and high crowned. Larger (presumed male) mandibles are generally more robust than in the Early Miocene east African forms but are not as strongly built as more thickly enameled taxa (Begun 2002). All species in which evidence is available display a relatively high root for the maxillary zygomatic process. Compared with *Proconsul* and other Early Miocene forms, *Dryopithecus* has reduced cingula, relatively short lower molars (Szalay and Delson 1979), expanded occlusal surfaces, and reduced molar crown flare and a mandibular symphysis reinforced by a prominent inferior transverse torus.

Until recently, the type species, *D. fontani* (11–12 Mya), was among the less well-known fossil hominoids cranially. New material from Catalonia, NE Spain (Moyà-Solà et al. 2009a, b), however, has dramatically improved our understanding of this chimpanzee-sized ape. A partial cranium dated to 11.8 Mya preserves several hominoid and hominid synapomorphies: a large nasal aperture with its widest portion located inferiorly and its margin constructed primarily of the maxilla,

Fig. 9 (*Upper*) Frontal and profile views of *Rudapithecus hungaricus* part skull (Photograph courtesy D. Begun). (*Lower*) Frontal and profile views of *Pierolapithecus catalaunicus* cranium (Photograph courtesy S. Moyà-Solà)

over a hard palate that is wide anteriorly. Unlike other large-bodied apes, however, the zygomatic slopes posteriorly from the orbital margin to the root, although there is mid-facial prognathism as well. The authors describe the steep face and vertical orientation of the nasal aperture as resembling extant *Gorilla*, in contrast to earlier stem hominoids with more sloping anterior maxillae. The subnasal morphology is stepped, as in extant hominines, but the premaxilla does not overlap the maxilla at the midline, which suggests a more primitive condition than that seen in *Nacholapithecus*. It has rather broader canines than other species, frequent cingula on the lower molars, while in larger mandibles the corpus shallows markedly from the symphysis toward the rear, unlike other species.

Rudapithecus

Although formerly placed in *Dryopithecus*, the slightly younger (9.5–10 Mya) *Rudapithecus hungaricus* (Kivell and Begun 2009) is also well known cranially (Fig. 9). Comparable in tooth size to *D. fontani*, it differs in its labio-lingually thicker incisors, narrower canines, reduced molar cingula, and more tapered M3. The mandibles have weak symphyseal tori, but the corpus is reinforced below M1–M2 by a lateral eminence. Cranial morphology is comparatively well known from several incomplete specimens from Rudabanya, Hungary (Begun and Kordos 1997;

Kordos and Begun 2001). The braincase is elongated, with a flat frontal displaying moderate postorbital constriction and strong anterior temporal ridges; supraorbital reinforcement is weak, but there is a fair-sized frontal sinus.

At the skull, rear inion is relatively highly positioned, while the mandibular fossa is transversely deep, with marked entoglenoid and postglenoid processes. The face is moderately projecting and deflected downward. The maxillary sinuses are larger than those of the East African fossils, and the nasal aperture has a broad base with subvertical sides. Again, in contrast to the early East African specimens where preserved, the subnasal floor is stepped, with the rear of the subnasal alveolar process extending over the palatal process of the maxilla, and an incisive canal is present. The long and projecting premaxilla is sagittally and transversely convex. The preserved semicircular canals suggest that *Rudapithecus* practiced relatively slow locomotion (Ryan et al. 2012).

Hispanopithecus

A smaller contemporary of *Rudapithecus* and also previously considered a species of *Dryopithecus* (Cameron 1997), *Hispanopithecus laietanus* is known from several sites in NE Spain (Begun 2002). Two partial skeletons have been discovered: a presumed male (39 kg) from Can Llobateres (Moyà-Solà and Köhler 1996) and a female (22–25 kg) from Can Feu (Alba et al. 2012). Mandibular teeth resemble those of *Rudapithecus*, but the premolars are relatively smaller, the molar cusps more rounded and expanded around the occlusal margins, and M_3 less tapered.

CLI-18800 preserves the upper dentition: the incisors are like those of *Rudapithecus*, the canines have strongly curved roots and narrow crowns, and the molar teeth increase in size posteriorly. In its known craniofacial structures, *Hispanopithecus* shows many similarities with *Rudapithecus*, including periorbital and maxillary morphology, the supraorbital region, frontal sinuses, and a locomotor pattern reconstructed as low, as determined via semicircular canal size. There are also contrasts, however, with CLI-18800 displaying a very high root for the zygomatic process and a relatively deep and flatter anterior aspect of the zygoma. The upper incisor row is more strongly curved, and the premaxilla is strongly biconvex. Overall the facial profile of *Hispanopithecus* is more concave.

The slightly earlier (c. 10.5 Mya) *H. crusafonti*, also from NE Spain, is known only from a mandible and some isolated teeth. Dentally slightly larger than *H. laietanus*, it is distinguished by comparatively broad upper canines, relatively longer upper premolars than in *Rudapithecus*, and relatively broader upper molars than *H. laietanus*. The mandible combines an exceptionally robust corpus with comparatively small tooth crowns; the symphysis is reinforced by a strong inferior transverse torus and the corpus bulges laterally below M1–M3. *Hispanopithecus* differs from the geographically close *Anoiapithecus* in that the molar crowns are relatively narrower, as are the buccal cuspulids, the hypoconulid is less centrally placed, and cingulids are lacking (Alba et al. 2012).

Overall, dental features of all three genera, such as relative shearing-crest development (Ungar 1996; Kay and Ungar 1997), pitting incidence of >35–<40 % (Ungar et al. 2004), thin enamel and dentine penetrance, and molar flare (Singleton 2003) accord with reconstructions of these forms as a frugivores, probably primarily soft-fruit feeders, in mildly seasonal subtropical forests (Andrews 1996). This is also consistent with mandibular corpus cross section which in many cases is like that of similar-sized *Proconsul*, although larger specimens resemble *Sivapithecus* in their shallow, more robust, and almost triangular section below M3 – proportions particularly effective in resisting torsion (Brown 1997) and raising the possibility of a tougher, more fibrous component in the diet of larger individuals to sustain their greater body bulk.

Anoiapithecus

Another new European Miocene form with a well-preserved cranium is *A. brevirostris*, known from the Middle Miocene (11.9 Mya) locality of Abocador de Can Mata in the Vallès-Penedès Basin of Spain (Moyà-Solà et al. 2009a). This unique short-faced taxon possesses the classic hominid features of a wide anterior palate, a nasal aperture widest at the base, but the upper premolars are moderately heteromorphic. There is also a frontal sinus, in which it differs from the condition seen in *Pierolapithecus*; the maxillary sinus is situated above the roots of the molars. The latter trait is considered to indicate a restricted sinus, but is often seen in extant hominoids that do not demonstrate reduced sinus volume. The molars themselves have thick enamel, cusps set toward the center of the tooth, small, compressed upper canines, and a robust mandible with a weak superior transverse torus. The extreme orthognathism and dentognathic traits could indicate a functional regime optimized for strong vertical crushing.

Pierolapithecus

The recently discovered Middle Miocene (12.5–13 Mya) partial skeleton of *Pierolapithecus catalaunicus* from Barranc de Can Vila 1, Els Hostalets de Pierola, Barcelona, Spain, provides extensive new evidence of European hominoids (Moyà-Solà et al. 2004). The specimen (IPS 21350) includes a virtually complete face and lower frontal, the upper dentition, and much postcranial material. The *Pierolapithecus* face is exceptionally prognathous compared with other Middle and Late Miocene Eurasian hominoids and, as such, is reminiscent of *Afropithecus*. It is low, with slender superciliary arches merging into a moderately swollen glabella region, below which the upper face is transversely flat. The orbits are broader than high, and the interorbital distance wide. In profile, the nasal bones are concave and salient over the wide piriform aperture, the inferior margin of which is well anterior to the tips of the nasal bones. The nasoalveolar clivus is high, convex, and markedly projecting. The deep, laterally expanded and strongly constructed zygomatics slope anteroinferiorly, with their root originating high above the alveolar margin of M^1. Internally, the paranasal sinus configuration of this taxon shows two specific similarities to extant *Pongo*: the maxillary sinus is limited in its anterior extent, but extends posteriorly toward the ethmoid, and the frontal sinus is absent (Pérez de los Ríosa et al. 2012). This, combined with the fact that the subnasal architecture does not include an overlapping premaxilla, suggests that *Pierolapithecus* bears no special relationship with extant African large-bodied apes, but may instead be part of the pongine clade.

The palate is short, wide, and deep, with the anterior dentition arcuate. I^1 is low crowned and procumbent, the large *C* low crowned and compressed. P^3 and P^4 are of similar size with reduced cusp heteromorphy, while M^1 and M^2 crowns are long and relatively narrow, with M^3 reduced. The lingual cusps are situated toward the crown edge and all the cheek teeth lack cingula.

This combination of dental and facial features distinguishes *Pierolapithecus* from all other Miocene hominoids; contrasts with *Dryopithecus* include the lower, more prognathous face; more anteriorly positioned zygomatic roots; shorter wider palate; larger, low-crowned anterior teeth; and relative molar crown size. In the view of Moyà-Solà et al. (2004), shared derived features of the two genera that link them to extant great apes include upper facial flatness, nasal bone projection and aperture form, a high zygomatic root, high nasoalveolar clivus, and deep palate. The postcranium also reveals shared derived traits with extant hominoids: a broad, shallow thorax and stiff lumbar region to the trunk, a dorsally positioned scapula, and apelike carpal bones with ulnar retreat from the wrist joint and evidence for the fibrous capsule of a semilunar meniscus, providing enhanced wrist abduction and supination. These traits, however, are combined with metacarpal and phalangeal features indicating the hand was palmigrade during locomotion and the fingers are short, as in monkeys, pointing to a dissociation in ape phylogeny between orthograde posture and climbing/below-branch suspension. The latter appears to have evolved later than the former and may well have arisen independently in several distinct lineages.

Similarities in craniofacial form and dental proportions with *Afropithecus* suggest a sclerocarp feeder, consistent with reconstructions of the *Pierolapithecus* habitat, based on the associated fauna, as wooded and relatively humid. Several Late Miocene hominoids (*Ouranopithecus*, *Ankarapithecus*, *Graecopithecus*) exhibit notably more ruggedly constructed crania and derive from drier, more fluctuating, and possibly more open environments.

Ouranopithecus

Ouranopithecus macedoniensis, represented by several jaws, teeth, and a fairly complete face from the c. 9-Myr-old northern Greek sites of Ravin de la Pluie, Xirochori, and Nikiti 1 (Fig. 10), is the largest European hominoid known, with males estimated to have been about female gorilla size. The face is strongly reinforced in its mid- and upper portions, pointing to powerful masticatory forces;

Fig. 10 (*Upper*) Frontal and profile views of *Ouranopithecus macedoniensis* part cranium (cast) (Photograph courtesy P. J. Andrews). (*Lower*) Frontal and profile views of *Ankarapithecus meteai* part skull (Photograph courtesy J. Kappelman)

the rectangular orbits are separated by a broad, stout interorbital area and laterally bounded by massive orbital pillars, while the nasal aperture is flanked by thick nasomaxillary (canine) pillars with broad, deep canine fossae beyond. The zygomatic region is very deep with, unusually for hominoids, a low origin for the zygomatic root on the maxilla. The premaxilla is strongly built, comparatively long, and markedly convex sagittally and transversely, with clivus, subnasal fossa, and incisive canal resembling *Dryopithecus*. The supraorbital torus bulges moderately above the orbits but less so medially; the strongly marked temporal lines indicate powerful anterior *temporalis* fibers.

The palate is deep and anteriorly broad; the incisors are set in an arc, offset from the other teeth by a pronounced diastema. The upper incisors are markedly heterodont, with the central teeth thick and broad and the laterals narrow and peg shaped; lower incisors are tall and slightly flared. Larger (male) canines are tall and laterally compressed but small when compared with molar size, while smaller (female) canines are very low crowned and almost premolariform.

Brown (1997) considers such low canines compatible with a greater degree of lateral mandibular movement than in modern apes. Both upper and (and especially) lower anterior premolars are triangular, the latter with a prominent mesial beak and lacking an anterior vertical honing facet from the upper canine. Instead wear occurs on the tip and along the protocristid, a feature judged reminiscent of *Australopithecus afarensis* (de Bonis and Koufos 2001). P^4 resembles P^3 in shape – another claimed *Australopithecus* – like trait and unlike other fossil and extant apes, while

P_4 is molarized, being elongate and with a high talonid. The molars are relatively large, with M^2 and M_3 the largest teeth; individual cusps are expanded, and both upper and lower rear molars possess accessory cusps. There is a marked wear gradient along the molar row: enamel is very thick and the cusps are worn almost flat before dentine appears.

Mandibles are robust, with thicker corpora than in extant apes, and larger (male) specimens are deep as well as thick. The symphysis is strongly reinforced by a broad, long planum and prominent inferior transverse torus. The lateral eminence originates opposite M_3, and the ramus ascends between M_2 and M_3. The gonial region is extensive and displays strongly marked ridging for the superficial masseter and medial pterygoid muscles. The condyle is relatively large and sagittally strongly convex.

Facial structure, muscle impressions, dental structure and proportions, occlusal morphology, and attritional wear gradients in *Ouranopithecus* all contrast with *Dryopithecus* and suggest extremely powerful masticatory activity, especially of the cheek teeth. This is further supported by microwear patterns which reveal a very high ratio of pits compared with striations on phase 2 facets of the cheek teeth (at >58 %, the highest of any fossil ape studied) and distinct wear on the incisors (Ungar 1996; Ungar et al. 2004), while the *Ouranopithecus* shearing quotient (and so relative shearing-crest development) is lower than that of any modern hominoid or other European fossil ape studied (Ungar and Kay 1995; Kay and Ungar 1997). In all these features, *Ouranopithecus* resembles extant hard-object feeders, pointing to exploitation of a similar niche – perhaps seeds, nuts, roots, and tubers, and other terrestrial vegetation. There are obvious resemblances here to some reconstructions of early (Plio-Pleistocene) hominine dietary niche(s), although these are unlikely to mirror any specially close phylogenetic link. De Bonis and Koufos (1997) argue that this model of *Ouranopithecus*' diet is consistent with reconstruction of its open habitat (De Bonis et al. 1992), although Andrews (1996) and Andrews et al. (1997) urge caution, considering the overall fauna to be undiagnostic other than indicating a strongly seasonal, possibly harsh, environment.

The poorly known *Graecopithecus freybergi* (von Koenigswald 1972), based on a single mandible from Tour la Reine, Pyrgos, Greece, and dated around 6.5–8 Mya, is often regarded as congeneric or even conspecific with *O. macedoniensis* (Martin and Andrews 1984; Andrews 1996), although Begun (2002) makes a strong case for its retention as a separate taxon based on molar size and mandible proportions.

Ankarapithecus

Ankarapithecus meteai (Ozansoy 1965), from sites in the Sinap Formation of Anatolia, Turkey, dated at c. 10 Mya, is a strongly built form known from cranial material including the type mandible and a partial face (Fig. 10), together with undescribed postcrania (Alpagut et al. 1996; Begun and Gulec 1998). The face is tall and markedly prognathic in both midface (unlike *Sivapithecus* and *Pongo*) and premaxillary regions. The clivus is biconvex, with large, low-crowned, and labiolingually thick central incisors and smaller lateral incisors. Male upper canines are relatively low crowned, and their roots form strong juga converging on the broad nasal aperture, with relatively shallow canine fossae beyond. The palate is deep, with the root of the zygomatic process set comparatively high above M^1 and into which the large maxillary sinuses extend. The vertically orientated, laterally flaring zygomatic process imparts strong anteriorly and laterally directed components to masseteric action, while the deep temporal fossa allows for a powerful *temporalis* muscle. The subnasal fossa is stepped and the incisive fossa large. The orbits are square, with a narrow interorbital space, very long nasal bones, broad, rounded orbital pillars, and prominent anterior temporal lines. Rather surprisingly in view of the rugged mid- and lower face, the superciliary arches above the orbits do not form a true torus.

The massive mandible is strongly buttressed, with a very deep, narrow, and vertical symphysis and the inferior traverse torus extending to the level of M_1. The rear of the corpus is very thick and the ramus broad. The lower incisors are labiolingually thick, narrow, and tall crowned, set almost vertically in a straight line between the low-crowned canines, which in males are more massive than in *Dryopithecus* or *Ouranopithecus* in basal section, while female canines are more premolariform, as in the latter genus. P_3 is large, oval, and elongated, with a large mesial beak comparable to *Dryopithecus* but smaller than *Ouranopithecus*, and P_4 is large and relatively broad, while M_1 is small relative to $M_{2.}$ Upper and lower molars are broader relative to their lengths than in other later Miocene forms; their occlusal surfaces have broad, flat cusps and shallow basins and lack cingula.

Andrews and Alpagut (2001) provide a valuable functional analysis of this taxon as a hard-object feeder in dry seasonal subtropical forest (Andrews 1996), illuminating aspects of *A. meteai* morphology and also that of other Miocene hominoids. In many features, *Ankarapithecus* resembles *Ouranopithecus*: dentally in the large, low-crowned and worn incisors; large cheek teeth; thick enamel; flat occlusal wear; poor shearing-crest development; and also in aspects of facial architecture and mandibular reinforcement. However, there are also differences: the supraorbital region differs, the *Ankarapithecus* interorbital region is narrower as are the lateral orbital margins, the midface is more prognathic, and the zygomatic root originates higher on the maxilla, while the mandibular corpus is massively thickened under the rear molars, so that it is actually broader than deep, whereas that of *Ouranopithecus* is deeper and narrower in cross section.

Oreopithecus

Oreopithecus bambolii, a comparatively large-bodied form dating from 6 to 7 Mya, is represented by multiple specimens from northern Italy, including a largely complete skeleton, making it the best-known European fossil primate. This has not prevented protracted debate about its affinities, although in recent years there has been a growing consensus that *Oreopithecus* is a primitive hominoid. Whatever its phyletic status, it is clear that *Oreopithecus* differs markedly in adaptive features and inferred niche from other Late Miocene European and West Asian hominoids.

The *Oreopithecus* skull combines a relatively small, low, but globular neurocranium with a deep, broad, and moderately projecting face that reflects anterior placement and projection of the midface and nasal region, for the premaxilla and clivus are short and comparatively vertical. The supraorbital torus is well developed, the interorbital region broad, and the nasal bones short and salient. Strong canine pillars are bounded by shallow canine fossae, while the zygomatic process is comparatively deep with a low, anteriorly placed root originating above P^4/M^1, and the zygomatic arch is long, flaring, and upwardly curved posteriorly. The alveolar region has deep but restricted sinuses. The saddle-shaped articular eminence is broad and long, with a large entoglenoid process. The articular and tympanic portions of the temporal are not fused, but the temporal petrous is hominid-like in its shallow, indistinct subarcuate fossa. The mastoid is broad and continuous with the extensive, strongly marked nuchal area. Zygomatic flare and mandibular proportions point to powerful, fleshy temporal muscles, as do the deep nuchal and sagittal crests, meeting high on the skull rear; the sagittal crest continues well forward before dividing into two prominent anterior temporal lines.

The strongly built mandible is large, with corpus height decreasing slightly along the cheek teeth row, and with strong reinforcement provided by the pronounced lateral eminence below the molar region. The ramus is broad and high with an expanded gonial region. There are pronounced markings for the masseters and medial pterygoids, while the condylar processes, below the broad and convex condyles, display strong markings for the lateral pterygoids.

Many of these cranial features can be considered representative of the primitive catarrhine morphotype (Harrison 1986); the exceptions are those features of the maxilla, zygomatic region, and mandible summarized above that can be related to masticatory power (see below). The dentition is highly derived: the incisor teeth are small overall and vertically implanted; those in the mandible are labiolingually compressed, while the uppers are heteromorphic with I^1 exhibiting a distinctive projecting lingual cusp. Canines are basally stout but not very tall and only loosely interlock, with a diastema small or absent. Larger (male) upper canines are strongly compressed and with a sharp rear edge, the lowers are more rounded in section; smaller (female) upper canines are rather incisiform. Much canine wear is from the tips; there was some C^1/C_1 honing, and some larger upper canines show evidence of slight honing against P_3, but smaller ones lack this, and the anterior face of C_1 did not hone against I^2. The lower premolars are bicuspid, with P_3 oval in outline and P_4 more rectangular; upper premolars are oval with subequal cusps. Upper and lower molars are elongated and bear tall, spiky cusps with deep notches between. Besides the four main upper molar cusps, a metaconule is positioned centrally on the crista obliqua, often linked to the hypocone by a crest. On the lower molars, the protoconid and hypoconid (buccally) and meta- and entoconid (lingually) are joined by sharp crests to a well-developed centroconid on the cristid obliqua, so mirroring the upper molars in their distinctive occlusal pattern. The hypoconulid is frequently split into several smaller cusps. M_1 usually bears a small paraconid, which is rarely present on M_2 and never on M_3. M_1 and M_2 are subequal in size, and M_3 is the largest tooth. The inner ear shows adaptations to medium-slow agility, somewhat more active than in *Rudapithecus*/*Hispanopithecus*, but marginally less so than *Proconsul*.

Although it displays some primitive features, the postcranial skeleton is apelike, indicating a degree of orthogrady, forelimb suspension, and strong grasping capabilities in the feet. The thorax is broad, the lumbar region short, and the iliac blades are short and broad, with a prominent anterior inferior iliac spine. The forelimbs are much longer than the hind limbs and display multiple adaptations to stability and hyperextension at the elbow joint and rotation in the forearm. There were a wide range of movements at the wrist, with short palms and long, curved fingers. The femora show weight-bearing adaptations at hip and knee, with flexible, wide-ranging movements at the ankle, and a short midfoot with long, strongly muscled digits including a powerful, opposed hallux.

Oreopithecus' reduced anterior dentition, expanded cheek teeth with complex occlusal morphology, relatively deep and orthognathic face, small neurocranium combined with large ectocranial crests and powerful chewing muscles, and robust mandible all point to a specialized folivorous diet of bulky, relatively low-grade food items which, judging by postcranial morphology and proportions, it exploited largely via an underbranch milieu. This conclusion is reinforced by study of relative shearing-crest development (Ungar and Kay 1995; Kay and Ungar 1997), which shows it to have the highest shearing quotient of any catarrhine studied, substantially in excess of any extant or other fossil hominoid. Further support is provided by dental microwear patterns, with a very low proportion (17 %) of pitting on phase II facets (Ungar 1996; King 2001; Ungar et al. 2004), consistent with extreme folivory. This wholly accords with reconstructions of *Oreopithecus*' paleoenvironment, which indicates lowland mixed broad-leaved and coniferous forest, with bushes, ferns, and sedges accumulated under swampy conditions (Andrews et al. 1997; Harrison and Rook 1997). However, see Alba et al. (2001) for an alternative and, to our minds, less convincing interpretation of the *Oreopithecus* skull based on biomechanical constraints associated with orthograde posture and bipedalism. These authors derive *Oreopithecus* cranial morphology from a *Dryopithecus*-like ancestor by a process of neoteny.

South and East Asia

Sivapithecus

The best-known Asian fossil ape genus is *Sivapithecus*, from Late Miocene (8.5–12.7 Mya) deposits in the Siwalik Hills of India and Pakistan and including material assigned to *Ramapithecus* prior to the 1980s (Pilbeam 2002). *Sivapithecus* is rare throughout the Siwalik record, comprising only c. 1 % of the mammalian community (Ward 1997). Despite this, aspects of its cranial morphology are relatively well known through discoveries over the last three decades; in particular,

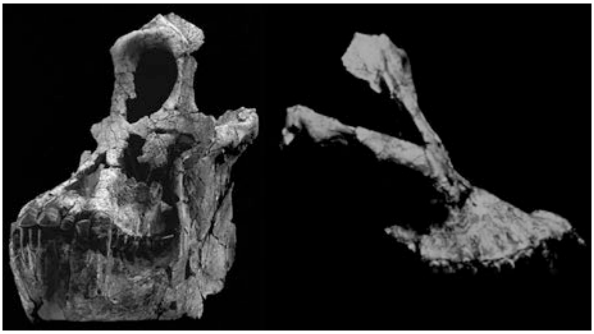

Fig. 11 Three-quarter frontal and profile views of *Sivapithecus indicus* (Photograph courtesy D. R. Pilbeam)

a partial skull (GSP 15000) from Potwar, Pakistan, provides much information on facial and gnathic morphology (Fig. 11). It consists of the left side of the face with zygomatic arch, palate, mandible, and complete adult dentition (Pilbeam 1982).

The specimen indicates many similarities with *Pongo* in its overall facial proportions (but see below): the orbits are taller than broad and high-set, ovoid in outline, and the zygomatic foramina are large. The interorbital distance is very narrow, while the lateral orbital pillars are slender, especially sagittally, and there are distinct supraorbital ridges but no continuous torus.

Postorbital constriction is marked, with the anterior temporal lines strongly convergent, implying a well-developed sagittal crest in larger individuals. The frontal rises more steeply above the orbits than in extant nonhuman African apes and is orangutan-like in its contour and the absence of a frontoethmoid sinus.

The nasoalveolar clivus is long and strongly curved, intersecting the alveolar plane at a shallow angle. As in the orangutan but in contrast to *Dryopithecus*, *Ouranopithecus*, and *Ankarapithecus*, the nasal floor is smooth, with the premaxilla curving into the nasal cavity and joining the palatal process without a step; the incisive fossa and incisive foramen are both tiny, linked by a very narrow incisive canal. The long, medially convergent canine roots are externally rotated, while the deep zygomatic process is thin and *Pongo*-like in its flare. These features result in exceptionally prominent canine pillars reinforcing the robust anterior midface and well-marked canine fossae lateral to them (Ward and Pilbeam 1983). The GSP 15,000 mandible is deep and strongly built, the symphysis exhibits pronounced buttressing, the corpus is of fairly constant depth along the tooth row, while the ramus is high and broadest at the level of the occlusal plane, tapering slightly superiorly. The facial contour is *Pongo*-like in its marked concavity, nasoalveolar clivus projection, superoposterior slope to the zygomatic process and lateral orbital pillar, and the upward inclination of the zygomatic arch itself.

Nonetheless, there are contrasts with the orangutan: the *Sivapithecus* midface is much longer, the nasal bones especially so, and the maxillary sinus is more restricted (Ward 1997). The mandible in particular contrasts with *Pongo* in most features other than its high ramus; while highly variable (Brown 1997), all *Sivapithecus* specimens display markings for the anterior digastric muscles which are absent in orangutans (see above), and the inferior transverse torus does not extend as posteriorly as in *Pongo* (Brown 1997). There are also contrasts in corpus cross section: *Sivapithecus* specimens have robust, broad corpora, ovoid below the premolars, more triangular below M_3, with smaller specimens relatively shallow, larger ones deeper. They show marked relief, with an intertoral sulcus near the lingual base below the cheek teeth, and a pronounced lateral eminence which continues to the base, whereas in orangutans the lateral eminence is usually a much less prominent swelling restricted to the upper part of the corpus. *Sivapithecus* mandible proportions have been interpreted as resisting sagittal bending loads on the balancing side and pronounced torsional and shearing loads on the working side, associated with powerful molar action and, as a possible secondary factor, incisal biting (Kelley and Pilbeam 1986; Brown 1997).

Dental features accord with this interpretation: the upper incisors are strongly heteromorphic, and the central teeth are very wide and spatulate with a heavily crenulated, extended lingual tubercle; the laterals are much narrower. The canines are moderately tall, compressed, and outwardly rotated and display only limited dimorphism. P^3 is larger than P^4, while the mandibular premolars are broad, with P_3 expanded mesiobuccally and displaying only limited evidence of upper canine honing. The thickly enameled molars lack cingula and display expanded, bunodont cusps and so limited occlusal foveae. In the upper jaw, M^2 is the largest tooth, while M_3 is the largest of the relatively short and broad lower molars. The cheek teeth are closely packed, with clear interproximal wear facets and, despite the thick enamel, often display a pronounced wear gradient with, in older individuals such as GSP 15,000, destruction of crown relief and extensive dentine exposure.

Overall, evidence points to *Sivapithecus* as a frugivore/hard-object feeder, possibly nuts, seeds, bark, or hard-pitted fruits, requiring powerful mastication by the postcanine teeth. Earlier scenarios of the genus as an open habitat form, exploiting terrestrial vegetation, have been replaced by reconstructions of its environment as predominantly seasonal tropical or subtropical closed-canopy forest or woodland, albeit with patchiness and expanding areas of more open grassland in the later phase of its presence in the Siwalik record (Andrews et al. 1997; Ward 1997). While this shift could reflect broader climatic changes that, through the contraction and break up of its forested habitat, eventually resulted in the extinction of *Sivapithecus*, it also might be the case that the taxon was more adapted to open habitats than previously thought. Analysis of some Siwalik carpals suggests that *Sivapithecus* may have been a knuckle-walker (Begun and Kivell 2011).

Three *Sivapithecus* species are recognized, differentiated primarily on dental proportions: *S. sivalenis* from Siwalik sites dating between 8.5 and 9.5 Mya is the type species. *S. indicus*, represented by GSP 15,000 and other material, is earlier (10.5–12.5 Mya) and with absolutely rather smaller teeth than *S. sivalensis*, but with a proportionately larger M_3 compared with M_2, and with a rather shorter premaxillary region. A humerus with a retroflexed and mediolaterally strongly curved shaft and a prominent deltopectoral crest is assigned to this species. *S. parvada* is a recently recognized, appreciably larger form, dating around 10 Mya. Its I^1 is particularly wide relative to its breadth, the premolars, especially the lower ones, are expanded relative to molar size, and M_3 is again much larger than M_2.

The mandible's symphysis and anterior corpus region are exceptionally deep, while a humerus referred to *S. parvada* broadly resembles that of *S. indicus* but is much bigger, implying larger body size overall.

Gigantopithecus

Many workers regard the Asian genus *Gigantopithecus* (von Koenigswald 1952) – known from massive mandibles and individual teeth from the Late Miocene/Pleistocene of southern China, Vietnam, and the Siwaliks of India and Pakistan – as closely related to *Sivapithecus*. While extremely large, it is characterized by a reduced anterior dentition, with relatively small lower incisors and low-crowned but basally large canines without honing facets, strongly worn down from the tip and functionally incorporated in the premolar/molar rows. The expanded premolars are strongly molarized: P^3 is bicuspid with a large talonid and is larger than P^4, which is almost square with a large trigonid taller than the talonid. The upper molars are almost square, the lowers elongated; all have very thick enamel, high crowns, and low cusps. The symphysis is reinforced by a moderate superior transverse torus and a much more extensive inferior torus that may extend as far back as M_1.

Gigantopithecus giganteus is known from specimens found from the 1960s onward from Haritalyangar and other Siwalik sites, especially a mandible CYP359/68 (Pilbeam et al. 1977), usually considered late in the Siwalik sequence at <7 Mya (Johnson et al. 1983). However, Pillans et al. (2005) argue for a date of 8.6 Mya for the mandible and report a newly discovered M^2 from the earlier (8.85 Mya) HD site at Haritalyangar which also yielded an incisor assigned to *Sivapithecus*, demonstrating sympatry of the two genera. Fossils of the more recent *G. blacki* are even larger than those of *G. giganteus*, with more pronounced molarization of the premolars, so that P_3 is more distinctly bicuspid and P_4 longer, while the molars are higher crowned, with low, expanded cusps, and multiple accessory cusplets. The mandibular symphysis is long and powerfully buttressed; the corpus is strongly reinforced by a thick lateral torus originating below M_1 and corpus depth increases posteriorly (Weidenreich 1945). Given these and other contrasts between the South and East Asian species, Cameron has recently reassigned the Haritalyangar mandible to *Indopithecus* (Cameron 2001, 2003; Pillans et al. 2005).

The size of *Gigantopithecus* fossils almost certainly precludes arboreality, and most reconstructions are of a ground-dwelling pongine exploiting a low-grade, bulky diet – perhaps bamboo (present at both Siwalik and Chinese localities) – although more varied diets, including fruits, have been suggested (Ciochon et al. 1990). Whatever the details, dental and gnathic features clearly indicate an extremely powerful masticatory apparatus with a premium on occlusal crushing and grinding by the cheek teeth, together with an anterior dentition capable of generating considerable bite forces for cropping food items. The short, premolariform canines, together with the mandible's symphyseal and corporal proportions, point to the generation of powerful torsional and shearing forces during food processing.

The same environmental changes that reduced forest and woodland cover, leading to the extinction of *Sivapithecus*, may well have favored the evolution of *Gigantopithecus* as a form better adapted to more open conditions and the exploitation of terrestrial vegetation (Ward 1997; Pillans et al. 2005).

Lufengpithecus

Lufengpithecus is another large-bodied Asian pongin, represented by extensive material, including several distorted crania and numerous teeth, from the Late Miocene (c. 8 Mya) of Lufeng, Yunnan province, southern China. Dental metrics indicate a degree of sexual dimorphism rather greater than that of any extant ape (Kelley and Qinghua 1991; Kelley 1993; Schwartz 1997). Cranial morphology contrasts with *Sivapithecus* in the relatively shorter midface, square orbits, broad interorbital and glabellar regions, and more prominent supraorbital torus above the medial superior orbital margins, resembling more the *Dryopithecus* pattern. The nasoalveolar clivus is relatively short and the mandibular symphysis strengthened by a moderate superior and strongly developed inferior transverse torus. The corpus is narrow and columnar with little sculpting or buttressing (Brown 1997), presumably resistant to vertical occlusal forces, but less well adapted to torsional or shearing forces generated by the cheek teeth.

The upper central incisors are tall and narrow but relatively thick and buttressed by a median pillar on the lingual surface, while the lower incisors are relatively narrow and moderately procumbent. Presumed male canines, especially the lowers, are tall, sharply tapering, and relatively slender. Molar enamel is moderately thick, and the crowns are narrow with the cusps situated toward the rim so that the foveae are extensive, and the occlusal surface bears a complex pattern of crenulations. Overall molar occlusal morphology is remarkably like that of the orangutan (Ward 1997), suggesting a frugivorous niche, as do the similarities with *Dryopithecus*. Paleoenvironmental indicators point to swampy moist tropical forest conditions, with ferns and epiphytes in which – again unlike *Sivapithecus* – *Lufengpithecus* was common, representing >33 % of the mammalian fossils (Andrews et al. 1997).

Kelley (2002) recognizes three species of *Lufengpithecus*: *L. lufengensis*, the type species, is the best known; *L. keiyuanensis* and *L. hudienensis* have smaller postcanine teeth and rather greater molar cingulum development than *L. lufengensis*, with *L. keiyuanensis* possibly also having thinner enamel.

Khoratpithecus

The recent discovery of teeth and a part mandible from Middle and Late Miocene deposits at sites in northern Thailand, and so within the geographical range of Pleistocene *Pongo*, sheds further light on orangutan ancestry (Chaimanee et al. 2003, 2004). The finds have been assigned to the new genus *Khoratpithecus* and display numerous dental and gnathic similarities with *Pongo*, as well as with

Lufengpithecus and, to a lesser extent, *Sivapithecus*. *Khoratpithecus piriyai* (9–7 Mya) is a large form (estimated 70–80 kg body weight) from a locality in Khorat, NE Thailand, and represented by a mandible body with the left canine – right I_2 roots – and with the right canine and all cheek teeth crowns preserved on both sides (Chaimanee et al. 2004). The symphysis is strongly sloping, thicker in overall cross section than usual in *Pongo*, with a weaker superior traverse torus, shallow genial fossa, and strongly developed inferior torus that, while wide and extending to below the anterior part of the M_1 crown, is less posteriorly extensive than in the orangutan. While the geniohyoid muscle facets are distinct, *Khoratpithecus*, like *Pongo*, lacks any impression for the anterior digastric muscle. The corpus is uniformly deep, with a marked depression on the lateral surface below the C/P_3 region and thickening posteriorly, accentuated by a pronounced lateral eminence below M_3.

Judging by anterior jaw proportions and alveoli, the procumbent incisors were larger than in *Lufengpithecus* but smaller than *Pongo* and arranged in a slightly convex arc. Enamel wrinkling, while present, is less complex than in the orangutan, the P_4 is shorter, and the molar cusps are more centrally located than in the modern ape. The site indicates a riverine setting with palms and dipterocarps, together with proboscids, anthracotheres, pigs, rhinos, bovids, and rare *Hipparion*, corresponding to the Upper Nagri/Lower Dhok Pathan Formation faunas in the Siwalik sequence.

An earlier species, *Khoratpithecus chiangmuanensis* (13.5–10 Mya), is based on upper and lower teeth of a single individual from Ban Sa in the Chiang Muan basin (Chaimanee et al. 2003). Enamel wrinkling, markedly heterodont upper incisors, P^3 crown form, lack of molar cingula and comparable degrees of relative enamel thickness, and dentine penetrance again align it with *Pongo*, but it differs from the latter in its smaller central incisors, in the weaker median lingual pillar of the upper and lower incisors, in the greater buccal flare of the lower molar crowns, and in its less intensive enamel wrinkling.

Contextual evidence associated with *K. chiangmuanensis* indicates a mosaic of tropical freshwater swamps and lowland forest that contrasts with the temperate flora from Lufeng, instead resembling modern African habitats such as those in the southern Sudan around the source of the White Nile. Chaimanee et al. take this to indicate a Middle Miocene floral and faunal dispersal corridor linking South East Asia and Africa that may have been critical in hominoid dispersion. Overall, *Khoratpithecus* closely resembles *Lufengpithecus* in its dentition, but its similarities with *Pongo*, especially the absence of digastric fossae, point to closer affinity with the modern genus than any other fossil ape.

Conclusions

Early Miocene hominoids already show considerable craniodental diversity, probably associated with dietary niche differentiation. Better known genera (*Afropithecus*, *Proconsul*) have contrasting morphologies but span a range of frugivory: *Proconsul* sp. and *Dendropithecus* were probably soft-fruit feeders, *Afropithecus* exploited hard-cased fruits. Among the less well-known genera, some (e.g., *Morotopithecus*, *Turkanapithecus*) bear cranial and/or dental similarities to *Afropithecus*, suggesting a hard-fruit niche, and that the most familiar cranial morphology – that of *Proconsul* – is not necessarily characteristic of many Early Miocene hominoids. *Limnopithecus* and *Micropithecus* appear to have been folivores on the basis of their dentition.

Middle and Late Miocene forms from the region (*Nacholapithecus*, *Equatorius*, *Kenyapithecus*, *Samburupithecus*) are thick enameled and probably hard-cased fruits and seed feeders, while environmental evidence suggests more open, rather drier, and more seasonal habitats. The more southerly *Otavipithecus* is an exception, with thin enamel and minimal dental wear, pointing to a soft-fruit diet.

By the Middle Miocene, hominoids are known from Europe and Western Asia. The earliest (*Griphopithecus*) are thick enameled, as are many later genera which are also generally more robust cranially than *Proconsul*, some especially so. At least one successful genus (*Dryopithecus*), however, has thin enamel and an only moderately strongly constructed cranium, although occlusal area, inferior symphyseal reinforcement, and, in larger individuals, mandibular cross section are expanded compared with *Proconsul*. *Dryopithecus* also contrasts with early East African fossils in its stepped nasal floor with the alveolar process overriding the palate and an incisive canal present. Overall, evidence suggests *Dryopithecus* primarily exploited soft fruits. The recently described, markedly prognathous *Pierolapithecus* is much more reminiscent of *Afropithecus* in its morphology and, as such, probably a sclerocarp feeder.

Broadly contemporary with the younger *Dryopithecus* species at 9–10 Mya, *Ouranopithecus* and *Ankarapithecus* are more strongly built forms whose cranial reinforcement, muscle markings, gnathic proportions, and dental features all point to impressive masticatory power and hard-object feeding, characteristics shared with the less well-known and rather younger *Graecopithecus*. Of about the same age (7–8 Mya) is the (masticatory power apart) generally contrasting *Oreopithecus*. This genus retains many primitive cranial traits together with features making for enhanced chewing capability and a distinctive dentition adapted to specialized folivory.

A similar trend to more robust morphologies is seen in South Asian hominoids, although details differ. The Late Miocene *Sivapithecus* (8.5–<13 Ma) is broadly *Pongo*-like in many aspects of cranial morphology, including periorbital proportions, mid-/lower facial prognathism and cheek orientation, nasal floor structure, and the presence of a narrow incisive canal, and remains among the most convincing instances of a comparatively close phylogenetic link between fossil and extant hominoid taxa, although *Sivapithecus* is unlikely to be directly ancestral to the orangutan. Cranial and dental features of *Sivapithecus* point to a frugivorous/hard-object feeding niche in increasingly patchy, fragmented habitats. These same environmental shifts probably underlie the appearance of *Gigantopithecus* [*Indopithecus*] *giganteus* in the Siwalik record, the oldest example of which is sympatric with *Sivapithecus*. *Gigantopithecus* mandibles are massive and powerfully reinforced, while occlusal area is expanded through increased molar size, premolar molarization, and incorporation of the low-crowned, worn flat canines into the cheek teeth rows. These features are evident in *G. giganteus* but even more pronounced in the later, East Asian, *G. blacki* (2–<1 Mya). Given its size, *Gigantopithecus* probably exploited bulky, low-grade terrestrial vegetation, with bamboo as the most likely predominant food source.

Also from East Asia and roughly contemporary with latest *Sivapithecus* and earliest *Gigantopithecus* is *Lufengpithecus*. In some respects, this is cranially rather reminiscent of *Dryopithecus*, contrasting with *Sivapithecus* in its broad upper face, supraorbital development and orbital proportions, thinner enamel, in its mandibular section which is less resistant to torsion and shear forces, and in its molar occlusal pattern which is more *Pongo*-like than that of *Sivapithecus*, all of which suggest a frugivorous diet.

The immediate ancestry of the extant great apes is obscure, while the entire early evolution of hylobatids is unknown. Both the distribution and diversity of contemporary *Hylobates* and *Pongo* populations indicate that climatic changes and associated sea-level fluctuations have been major determinants of their evolution over the last 2+ Ma. *Pongo* in particular is cranially highly variable: there are appreciable differences between Bornean groups separated by major river barriers, as well as marked contrasts between these and Sumatran orangutans, leading to recent proposals for species-level distinction between the two island populations. All orangutans lack the anterior digastric muscle, thereby contrasting with virtually all other hominoids including *Sivapithecus*, which does, however, share with *Pongo* a distinctively airorhynchous cranial form. The recently discovered Middle/Late Miocene *Khoratpithecus* from Thailand displays jaw and dental affinities with *Sivapithecus* and especially *Lufengpithecus* and *Pongo*, sharing with the last a lack of any indication of the anterior digastric muscle.

The notably klinorhynchous African apes contrast in this respect and exhibit multiple similarities that indicate a common cranial pattern differentiated by varying growth periods. Since a degree of airorhynchy seems common among fossil hominoids and differentiates hominoids from non-hominoids, the African ape condition appears derived. Despite the comparatively full Miocene fossil record, there are no especially convincing candidates for modern African ape ancestry, although *Chororapithecus* is a potential link. The sequence and timing of splitting of the gorilla, chimpanzee, and hominin clades is uncertain, although some evidence (dental, gnathic, temporal) suggests that *Gorilla* is more primitive and *Pan* more derived. Differentiation of bonobos and chimpanzees and of east and west gorilla populations perhaps occurred in the Late Pliocene/Pleistocene. Recently recovered fossil teeth provide evidence of *Pan* (probably *P. troglodytes*) from c. 0.5 Mya in the East African Rift.

While there are broad associations between African ape diet and cranial form, more detailed analyses fail to show an exact correspondence, in part because of dietary variability and also because of cranial variation. Evidence suggests that cranial features are less closely determined by diet than are characteristics of the dentition.

Bonobos show reduced levels of sexual dimorphism in craniodental features compared with chimpanzees, perhaps reflecting differences in sexual behavior and social organization. Surprisingly, bonobos are *relatively* the most robust of the African apes in some cranial traits, gorillas *relatively* the most gracile. When viewed in the broader context of the hominoid fossil record, all the living great ape crania are comparatively lightly constructed, raising issues about their representative nature or otherwise for the functional and adaptive modeling of earlier hominoids.

Cross-References

- ▶ Dental Adaptations of African Apes
- ▶ Estimation of Basic Life History Data of Fossil Hominoids
- ▶ Evolution of the Primate Brain
- ▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
- ▶ Fossil Record of Miocene Hominoids
- ▶ General Principles of Evolutionary Morphology
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Great Ape Social Systems
- ▶ Modeling the Past: Archaeology
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Paleosols
- ▶ Postcranial and Locomotor Adaptations of Hominoids
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Primate Intelligence
- ▶ Primate Life Histories
- ▶ Quaternary Geology and Paleoenvironments
- ▶ The Biotic Environments of the Late Miocene Hominoids
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Dental Adaptations of African Apes

Mark F. Teaford and Peter S. Ungar

Contents

Abstract

Improvements in the primate fossil record, and in methods of data acquisition and analysis, have set the stage for new insights into the development, function, and evolution of hominoid teeth. This chapter is a brief review of recent advances. In essence, genetic analyses are changing our perspectives on the

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M.F. Teaford (✉)
Department of Physical Therapy, High Point University, School of Health Sciences, High Point, NC, USA
e-mail: mteaford@highpoint.edu; mteaford@jhmi.edu

P.S. Ungar
Department of Anthropology, University of Arkansas, Fayetteville, AR, USA
e-mail: pungar@uark.edu

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evolution of morphology, while improved studies of dental development and microstructure have yielded permanent markers of developmental history and microstructural differences of functional significance. More realistic perspectives on the physical properties of foods are yielding new functional interpretations of differences in tooth size. Finally, landmark-free analyses of tooth shape and wear are giving researchers the chance to actually monitor how teeth are used in living primates and by extrapolation in fossil primates too. Through techniques such as these will come a better understanding of the intricacies of dental function and a clearer picture of our past.

Introduction

People have been fascinated by the similarities between apes and humans ever since the first reports of apes filtered out of Africa. Linnaeus struggled to incorporate them into his *System of Nature*, but anatomical studies by Tyson (1699) and Huxley (1863), among others, forced the world to recognize the striking resemblance between African apes, in particular, and modern humans. Now, with the ape and human fossil record raising more questions and technological advances generating new perspectives on morphology, it is time to take another look at the teeth of African apes, to see what is known and not known about them.

Dental Development

Some of the most revolutionary discoveries in all of morphology have come in the areas of genetics and dental development, where subtle genetic changes have been shown to have major impacts on morphology (Jernvall 2000; Salazar-Ciudad et al. 2003). Thus far, studies have been restricted to laboratory animals such as rodents, but the potential impact on studies of morphological change in ape and human evolution is immense. With that point in mind, what do we know about dental development in the African apes? Methods of data collection have sometimes overlapped and sometimes varied dramatically, but some general trends are still evident in the literature.

Longitudinal data for nonhuman primates are rare, and this is certainly true for studies of dental development in apes, where methods of monitoring crown and root development have generally involved either detailed dissections or radiographs of different individuals of known ages (e.g., Zuckerman 1928; Dean and Wood 1981; Swindler 1985; Beynon et al. 1991; Conroy and Mahoney 1991; Kuykendall 1996; Winkler 1995) (although see Anemone et al. 1991 for an exception to this). Net results have included estimates of the timing of tooth calcification and emergence and differences between teeth in those events. Analyses of chimpanzees have been far more common than those of other apes, due largely to the fact that chimps are often used in laboratory research. Ultimately, results are frequently compared with those for humans.

Estimates of the timing of tooth and root calcification have yielded some consistent similarities between apes and humans, but also some differences. Specifically, dental development in apes is completed much more quickly than in humans, at approximately 11–12 years as compared with approximately 18–20 years (Nissen and Riesen 1964; Conroy and Mahoney 1991; Kuykendall 1996). Yet apes and humans have fairly similar patterns of cusp initiation and tooth mineralization (Swindler 1985), and each tooth crown takes about the same time to develop (Dean and Wood 1981; Beynon et al. 1991). So how can the teeth of humans take longer to finish their development when individual human and ape tooth crowns take similar times to develop? First, there are significant differences in the degree of overlap between the development of certain teeth in apes and humans. For instance, in humans, each of the permanent molars completes its crown development before the next molar crown begins to develop. In apes, by contrast, there is a great deal of overlap in the timing of development of the molars (Reid et al. 1998; Dean 2000). A second factor helping to explain the faster completion of dental development in apes is a quicker rate of root growth after crown completion (Anemone et al. 1991, 1996; Simpson et al. 1992; Kuykendall 1996; Reid et al. 1998).

Finer-resolution differences in dental development may ultimately be discernible, both within and between species – e.g., differences between the sexes in some tooth mineralization stages (Kuykendall 1996) or differences in the formation time of specific molar cusps (Reid et al. 1998). However, additional resolution has also required further refinement of techniques (Winkler 1995; Beynon et al. 1998; Reid et al. 1998) which is now yielding additional insights. For instance, while the sequence of emergence of some teeth may distinguish bonobos from common chimpanzees (Bolter and Zihlman 2011), the relative timing of crown and root formation may not differ significantly between them (Boughner et al. 2012).

The net result of all of these developmental events is a complex pattern of sequences that can, by itself, be used to gain insights into primate life history (Smith 1991, 1994; see also chapter "▶ Primate Life Histories," Vol. 2) and morphological development (Boughner and Dean 2008). Schultz (1960) recognized a basic distinction between relatively rapid- and slow-growing primates, with the former gaining all of their permanent molars before the eruption of more anterior permanent teeth. Hominoids are all relatively slow growing, but variations in their sequences of dental eruption (so-called tooth sequence polymorphisms) (Garn and Lewis 1963) can still yield insights. For instance, comparisons of humans and common chimpanzees show that humans have much greater variability in the eruption of their canines and lower central incisors, whereas chimpanzees show greater variability in the eruption of their second molars (Smith 1994). Still, if the actual timing of dental eruption can also be calculated (see section "Incremental Microstructural Features" below), then the eruption of most pairs of teeth is highly correlated (Smith 1989), and the eruption of the first and last permanent teeth is, in turn, highly correlated with other life history variables (see chapter "▶ Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1).

Dental Microstructure

Dental enamel is formed of hydroxyapatite crystals bundled together into prisms which are, in turn, often woven together in complex patterns, including radial enamel and decussating Hunter-Schreger bands (Martin et al. 1988; von Koenigswald and Clemens 1992; Rensberger 1997; Maas and Dumont 1999). This inherent complexity has left researchers with a wealth of research possibilities, ranging from permanent markers of developmental history to structural anisotropy of functional significance.

Incremental Microstructural Features

Close examination of enamel prisms has revealed so-called cross-striations (periodic thickenings) laid down in a circadian fashion (Schour and Hoffman 1939; Massler and Schour 1946; Boyde 1964). This, coupled with surface markers known as perikymata, has allowed researchers to estimate the amount of time necessary for crown completion in modern hominoids (Dean and Wood 1981; Beynon et al. 1998; Reid et al. 1998; Shellis 1998; Dean 2000). But it has also given insights into tooth formation time and age at death in fossils (Bromage and Dean 1985; Beynon and Dean 1988; Dean et al. 1993, 2001; Smith et al. 2010), thereby suggesting that most of the early hominins (including the earliest members of our genus) had a more rapid "ape-like" pattern of dental development that did not begin to change until the Middle Paleolithic. Recent methodological advances, most notably in the area of nondestructive synchrotron microtomography (Tafforeau and Smith 2008; Tafforeau et al. 2012), raise the possibility of a far better understanding of dental microstructure across teeth in any primate taxon.

Enamel Prism Patterns

Before histological studies of the timing of dental development, researchers felt that the shape of prisms in prepared tooth sections ("prism packing patterns") could be used in phylogenetic studies, as certain patterns might be characteristic of certain taxonomic groups (Shellis and Poole 1977; Gantt 1979, 1983; Xirotiris and Henke 1981). However, subsequent work showed that results were often dependent on methods of specimen preparation (Boyde et al. 1978; Vrba and Grine 1978). Detailed analyses of enamel at controlled depths subsequently suggested that hominoids might exhibit an unusual preponderance of "type 3" enamel (Boyde and Martin 1982; Martin et al. 1988). In this pattern, prism cross sections are open at the base. However, more work is still necessary to document the range of possibilities within and between large samples of teeth.

Enamel Thickness

One obvious result of the complex process of tooth formation in most mammals is an enamel cap covering the tooth crown – a cap that can vary rather dramatically in thickness. Studies of molar enamel thickness in hominoids have gradually progressed from simple linear measurements (e.g., Gantt 1977; Molnar and Gantt 1977; Kay 1981) to more complex measures designed to account for differences in body size (e.g., Martin 1983, 1985; Kono 2004; Smith et al. 2005, 2012; Gantt et al. 2006; Kono and Suwa 2008; Olejniczak et al. 2008). Given the complexity of crown shape and development, it is perhaps no wonder that there have been ongoing discussions about proper methods of analysis (e.g., Grine 1991; Macho and Thackeray 1992; Macho and Berner 1993; Macho 1994; Dumont 1995; Grine 2002, 2005; see also chapters "▶ General Principles of Evolutionary Morphology," and "▶ Virtual Anthropology and Biomechanics," Vol. 1). However, recent work has begun to refine the understanding of enamel thickness, as researchers move from summary characterizations of hominoids having relatively thin molar enamel compared with that of modern humans (Shellis et al. 1998) to more subtle differences in enamel distribution across molar tooth crowns (Schwartz 2000; Kono 2004; Smith et al. 2005; Kono and Suwa 2008; Constantino et al. 2009). Of course, along with such differences come questions of the functional significance of those differences. Given the inherent complexity of primate foods and diets (see chapter "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition," Vol. 2), it is not surprising that the correlation between enamel thickness and diet is not a perfect one (Maas and Dumont 1999), nor that the physical and chemical properties of enamel may vary within the tooth crown (Cuy et al. 2002; Lee et al. 2010) but surprisingly little between species (Constantino et al. 2012). This has led some to suggest that these properties are "highly conserved" in primate evolution (e.g., Constantino et al. 2012). Over the past two decades, conventional wisdom has dictated that thick enamel enabled primates to consume either more abrasive foods (Molnar and Gantt 1977; Rabenold and Pearson 2011) or harder ones (Kay 1981; Dumont 1995). However, that perspective is changing, largely because researchers are gaining a better appreciation for the functional implications of the structural complexity of enamel. On the one hand, prism decussation serves as an admirable crack-stopping mechanism (Pfretzschner 1986; von Koenigswald et al. 1987; Rensberger 1993, 2000; Maas and Dumont 1999) and thus may be a correlate of hard-object feeding in some situations (Martin et al. 2003; Lucas et al. 2008). On the other, not all tooth cracks originate from the occlusal surface (Lucas et al. 2008). Thus the distribution of enamel, and its decussation, may also be a correlate of feeding on hard *or* abrasive objects (Constantino et al. 2009). In either case, differences in the structure and properties of molar enamel in African apes are beginning to be tied to differences in so-called fallback foods (Lambert 2007; Marshall and Wrangham 2007; see also chapter "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition," Vol. 2) as chimps pursue softer foods while gorillas pursue tougher foods when preferred resources are not available (Constantino et al. 2009). Finally, we cannot forget that enamel *thinness* can be selected for too, for surface sculpting to form sharp edges when wear breaks through to the softer dentin (Ungar 2008).

Tooth Size

Measurements of tooth size have been the focus of some classic studies of ape and human dentitions (e.g., Ashton and Zuckerman 1950; Schuman and Brace 1955; Garn et al. 1965; Pilbeam 1969; Mahler 1973; Johanson 1974; Swindler 1976). However, while some interspecific and intraspecific differences in tooth size are undoubtedly associated with differences in body size (Garn et al. 1968; Gingerich et al. 1982; Conroy 1987), the more intriguing trends are those differing from the standard assumption that larger animals have concomitantly larger teeth that scale one to one with body size. Similarly, the degree and pattern of variation in tooth size may also be informative.

For instance, investigators have long known that humans have relatively small canines compared to modern apes (e.g., Gregory 1922). However, among modern apes, chimpanzees and orangutans have relatively larger incisors than do gorillas and gibbons (Jolly 1970; Hylander 1975; Kay and Hylander 1978). As a result, differences in incisor size may reflect differences in the degree of incisor use in ingestion (Ungar 1996).

*Intra*specific differences in canine size have also been used as indicators of sexual dimorphism, with gibbons and humans showing relatively little sexual dimorphism, and chimps, bonobos, gorillas, and orangs all showing significantly more (Ashton and Zuckerman 1950; Johanson 1974; Swindler 1976; Kinzey 1984). This has led to further inferences about differences in social behavior (e.g., Kelley 1986; Plavcan 1990; Plavcan et al. 1995; Plavcan and van Schaik 1997), with, for instance, species showing high degrees of sexual dimorphism also showing polygynous mating systems (see chapters "▶ Great Ape Social Systems," and "▶ Cooperation, Coalition, Alliances," Vol. 2).

However, if analyses of tooth size are going to move from simple correlations (between morphological and behavioral differences) to explanations of causation, they need to be based on a better appreciation of the complexities of such relationships. In the 1970s, discussions began on the exact nature of the relationship between tooth size and body size, with initial studies suggesting close ties between postcanine tooth area and body metabolism (Pilbeam and Gould 1974; Gould 1975) but subsequent analyses showing such a relationship to be grossly oversimplified (Kay 1975; Fortelius 1985). The confounding variables apparently come in three forms. First, different analytical protocols have suggested different scaling relationships between tooth size and body mass in primates independent of anything else (Smith 2009; Copes and Schwartz 2010; Ungar 2014). Second, analyses of modern primates have shown that the relationship between diet and food processing is extremely complicated (Fortelius 1985; Lucas 2004). Thus, for example, both the rate of chewing and the physical response of food to chewing may influence the relationship between tooth size and diet. And third, analyses of fossil primates have shown that phylogenetic history may also complicate analyses of tooth size (Kay and Ungar 1997; Ungar 2002). For instance, the average Miocene ape incisor is narrower than that of modern apes. Perhaps Miocene apes had a different morphological starting point than extant apes, rather than simply being more folivorous (see chapters "▶ Fossil Record of Miocene Hominoids," "▶ The Biotic Environments of the Late Miocene Hominoids," Vol. 2 and "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3).

Work by Lucas and co-workers (Lucas et al. 1986; Lucas 2004) has brought another perspective to the discussion of the functional implications of differences in tooth size. In essence, anterior teeth and postcanine teeth are probably responding to different types of functional demands and thus need to be treated differently. Anterior tooth size is linked to the size of ingested particles, whereas posterior tooth size may depend on the deformability of the food, including a variety of properties like stickiness, particle shape, etc. Thus, perhaps relative differences in tooth size between incisors and molars in modern apes are giving more subtle clues about the dietary differences between species. For instance, the fact that the gorilla has relatively small incisors compared to its molars may *not* simply indicate less reliance on the incisors in ingestion. It may also reflect the fact that the molars of gorillas often process relatively small food particles that are not very sticky (Lucas 2004). Clearly, however, more work is needed on the relationship between tooth size and the properties of foods.

Dental Morphology and Wear

As Aristotle noted nearly two and a half millennia ago in *De Generatione Animalium*, tooth form reflects function. Studies of mammalian dental functional morphology do not date back quite that far, but they certainly boast a long and celebrated history nonetheless (Owen 1840; Gregory 1922). Early work on mammalian teeth, for example, suggested that their molars evolved to improve mechanical efficiency for particular masticatory movements (Simpson 1933; Crompton and Sita-Lumsden 1970; Kay and Hiiemae 1974). Subsequent work has continued to push this biomechanical perspective forward, focusing on relationships between tooth shape, on the one hand, and the strength, toughness, and deformability of foods on the other (e.g., Kay 1975; Rosenberger and Kinzey 1976; Seligsohn and Szalay 1978; Strait 1993; Lucas and Teaford 1994; Spears and Crompton 1996; Yamashita 1998; Lucas 2004; Lucas et al. 2004). In essence, primates that specialize on tough foods, such as insect exoskeletons and mature leaves (foods that are difficult to fracture), generally have reciprocally concave, highly crested molars for shearing and slicing. In contrast, those that prefer hard, brittle foods (those that resist initial puncture but are easy to fracture once a crack has started), such as many seeds, nuts, and palm fronds, tend to have rounder, flatter molar teeth for processing such items. Such contrasts, however, have left African apes somewhere in between these two extremes, with members of the genus *Gorilla* leaning slightly towards more crested molars as compared with members of the genus *Pan*. Of course, such morphological differences are ultimately due to a complex mix of phylogeny and function, where one factor might, once again, complicate the interpretation of the other (Rensberger 1973; Kay 1975; Maier 1984; Hartman 1989; Uchida 1998; Butler 2000). Thus, quantification and statistical comparison were to prove essential in deciphering these interrelationships.

Quantifying Functional Aspects of Tooth Form

Innumerable quantitative methods of characterizing tooth shape have been developed over the past few decades. Early investigations used length/width measures of teeth to compute basal areas of teeth and cusps, which were then used as indicators of tooth "shape" (e.g., Biggerstaff 1969; Corruccini 1977, 1978; Lavelle 1978). While initial efforts focused on documenting differences between taxa, with an eye towards discrimination of fossil taxa (e.g., Wood and Abbott 1983; Wood and Engelman 1988), elaborations of this approach have led to possible insights into intraspecific dietary variations within *Pan* and *Gorilla* (Uchida 1992, 1996, 1998).

Meanwhile, studies of chewing efficiency in primates (Kay and Hiiemae 1974; Walker and Murray 1975; Sheine and Kay 1977) prompted a series of classic papers delving into the functional significance of variations in occlusal morphology (Kay 1975; Rosenberger and Kinzey 1976; Maier 1977; Osborn and Lumsden 1978; Lucas 1979).

These have then spawned many attempts over the past few decades to characterize/measure the shape of features on the occlusal surfaces of teeth (e.g., Seligsohn and Szalay 1978; Teaford 1983; Hartman 1989; Pilbrow 2003; Ungar and M'Kirera 2003). The most well known of these is still probably Kay's Shearing Quotient (SQ) method for analysis of molars (Kay 1978, 1984). The lengths of mesiodistal crests are measured on unworn molars of several closely related species with similar diets. A least-squares regression line is fit to summed crest length and mesiodistal occlusal surface length in logarithmic space. SQs are computed as residuals or deviations from the regression line. This approach tracks diets of living apes fairly well, as the more folivorous siamang and gorilla have relatively longer shearing crests than do extant frugivorous hominoids (Kay 1977; Kay and Ungar 1997).

Spears and Crompton (1996) have suggested an alternative approach, measuring great ape cusp slopes from molar cross sections. They found that gorillas had high-angled occlusal surfaces, orangutans had gradually sloping surfaces, and chimpanzees had shallow "supporting" cusps but steeper "guiding" slopes. These findings are taken to suggest that orangutans are adapted to reduce a hard/brittle diet, whereas gorillas can more efficiently fracture small food particles by shear. Chimpanzees, on the other hand, seem to be better suited to a diet with a wide range of mechanical properties.

Still, with advancements in data collection and analysis (e.g., dental topographic analysis, geometric morphometrics, and finite element modeling), there will undoubtedly be an upsurge in morphological analysis that will yield new insights. For instance, recent finite element analyses emphasize that variations in occlusal morphology must also strike a balance between chewing mechanics and stress resistance (Berthaume et al. 2010; Benazzi et al. 2013). This should give pause for thought in thinking about functional differences in tooth shape among African apes, as those differences may not be so easily tied to differences in chewing efficiency.

Of course, most of what has been done thus far has focused on *molar* occlusal shape. Some of that is due to the fact that the anterior dentition has a simpler morphology than that of the molars, and some is due to the fact that we have a better understanding of how primates use their cheek teeth. Thus, despite the aforementioned studies pointing to differences between taxa in incisor size (Jolly 1970; Hylander 1975; Kay and Hylander 1978), little more had been done on incisor morphology until recently. Pilbrow has now documented differences between apes in the incidence of discrete/nonmetric traits, but the functional significance of those differences has yet to be examined (Pilbrow 2006). However, Deane (2009) has recently used measures of incisor crown curvature as an indicator of diet differences among modern apes, and these measures show some promise in allowing more robust functional interpretations, with, for example, chimpanzees showing more pronounced curvature than gorillas. Of course such interpretations are only as good as our knowledge of how these teeth function.

Analyses of canine size and shape have been used primarily in taxonomic work and in studies of sexual dimorphism (e.g., Leutenegger and Shell 1987; Wood et al. 1991; Plavcan 1993; Plavcan and van Schaik 1993; Kelley 1995; Kelley et al. 1995). Still, more recent work has begun to sort through the functional implications of variations in canine morphology (e.g., Plavcan and Ruff 2008; Deane 2012), many of which may hinge upon interspecific differences in gape and display rather than diet, especially in African apes.

Premolars, by contrast, are a bit of an enigma. Their shape often rivals that of molars in its complexity. They often bracket a functional transition in the dentition between the anterior dentition focused on ingestion and the posterior dentition focused on mastication (Wood and Uytterschaut 1987; Greenfield and Washburn 1992). However, after a series of initial studies of interspecific differences in the length and breadth or premolar crowns and crown components (e.g., Corruccini 1977, 1978; Wood and Uytterschaut 1987), little else has been done with their morphology. Recent debates surrounding the dental adaptations of the early hominins (e.g., Strait et al. 2009, 2012, 2013; Grine et al. 2010, 2012; Daegling et al. 2013), in particular, the importance of premolar food processing, is beginning to spawn new research in this area (e.g., Delezene et al. 2013).

Tooth Wear Analyses

While studies of tooth morphology give glimpses of the complex relationship between primate tooth shape and diet, most such work has been limited to unworn teeth. This is a major limitation because it leads to an incomplete picture of the form-function relationship. Wear is a normal phenomenon that begins as soon as a primate's teeth come into occlusion. Thus, natural selection should also act on worn teeth, favoring morphologies that wear in a manner that keep them mechanically efficient for fracturing foods (Kay 1981, 1985; Teaford 1983; Teaford and Glander 1996; Ungar and Williamson 2000). In essence, since tooth wear occurs throughout an animal's lifetime, a great deal of information will be missed if worn teeth are excluded from future analyses. Another limitation of studies that depend exclusively on unworn teeth is the lack of sufficient numbers of specimens for many (especially fossil) taxa. For instance, the entire published sample of early hominins from South Africa still boasts less than ten unworn M_2s (the teeth most often used in functional studies).

The tooth wear of apes has occasionally been the focus of work in previous investigations. Early studies examined the *degree* of tooth wear in apes and humans in attempts to correlate tough, abrasive diets with the presence of increased tooth wear (Black 1902; Campbell 1925; Schultz 1935; Ashton and Zuckerman 1950; Welsch 1967). As noted by Wolpoff (1971), however, such interpretations are complicated by the complexities of diet and mastication, not to mention methodological difficulties associated with incorporating differences in dental eruption timing into such analyses.

Some investigators have made more detailed comparisons along the tooth row, noting, for example, that chimpanzees exhibit heavier incisor wear than do other apes (Ashton and Zuckerman 1950; Welsch 1967), again suggesting heavier incisor use in chimpanzees. More recently, Dean et al. (1992) have noted that later-erupting molars in chimpanzees and gorillas may actually show heavier wear than their predecessors, suggesting that occlusal loading is greatest on the last molar in the tooth row. It is perhaps no wonder then that molars in these species may also exhibit compensatory eruption as wear progresses (Dean et al. 1992) similar to that documented for some human populations (Whittaker et al. 1982, 1985).

With the advent of cineradiographic and electromyographic studies of mastication, studies of molar wear facets began to document subtle differences in jaw movement between primate species, with modern apes generally showing an increased emphasis on crushing and grinding as compared with some other catarrhines (Kay 1977; Maier and Schneck 1981). With these suggestions, analyses of tooth wear took another crucial step towards deciphering the relationship between dental form and function. This type of work has since been brought into the twenty-first century through a combination of laser scanning and metrology software that now allows quantification of wear facet patterns on teeth, in what is now referred to as "occlusal fingerprint analyses" (OFA) (Kullmer et al. 2009). Interestingly, virtually all of this work to date has focused on analyses of fossil material, yielding insights into possible functional differences between populations (e.g., Fiorenza and Kullmer 2013) and modifications of fossil reconstructions (e.g., Kullmer et al. 2013). What are now needed are analyses of extant primates, to see if, for instance, differences in these patterns of wear might indicate even more subtle differences in jaw movement and/or tooth use.

Of course, OFA essentially works with slightly worn teeth (e.g., those with wear facets but not massive dentin exposures). If it *does* yield insights into dental function in apes, could larger-scale differences in wear-related changes in tooth *shape* yield even more information? A look through the literature reveals a striking paucity of such studies. Why? Quite simply, it is not easy to measure tooth shape on worn teeth. Traditional dental morphometrics depend on measuring distances between landmarks that are quickly obliterated by wear. Smith (1999) attempted to control for wear using a technique modified from Wood and coauthors (Wood et al. 1983). Molar occlusal views were captured on video and individual cusp areas were identified on a computer screen by mouse-driven cursor. This allowed calculation of relative 2D (planimetric) areas of cusps on unworn to moderately worn teeth (as long as cusp boundaries were identifiable). Smith's results suggest that cusp proportions do indeed reflect diet to some degree – e.g., chimpanzees are linked with gibbons, rather than with gorillas.

Even this approach though, is not ideal. First, specimens must still be sufficiently unworn to distinguish individual cusp boundaries, and these disappear pretty quickly, especially on thin enameled molars, such as those of chimpanzees and gorillas. More importantly, planimetric area studies do not adequately characterize the third dimension of dental morphology. This is a problem because mastication occurs in a 3D environment, and two teeth with similar projected 2D areas may differ greatly in cusp relief.

The ability to collect elevation data is vital to studies of dental functional morphology. If cheek teeth are indeed guides for jaw movements (Simpson 1933; Crompton and Sita-Lumsden 1970; Hiiemae and Kay 1972), then surface relief is critical to the angle of approach of mandibular and maxillary teeth as facets come into occlusion during mastication. This in turn determines the biomechanical efficiency with which items of given mechanical properties are fractured (e.g., whether foods are sheared or crushed).

Clearly, what has been needed is a way to consider worn teeth in 3D studies of dental functional morphology. Dental topographic analysis is now beginning to serve that purpose. Elevation data representing an occlusal surface are collected using a 3D scanner, and the tooth is modeled and analyzed using geographic information systems (GIS) software (Zuccotti et al. 1998; Jernvall and Selänne 1999) (Fig. 1). Because dental topographic analysis does not depend on specific landmarks for measurement, it is equally useful for measuring unworn and worn teeth.

Some results for studies of living great apes are summarized and combined here to provide an example. Ungar and co-workers studied dental topography of *Gorilla gorilla gorilla* and *Pan troglodytes troglodytes* (Ungar and M'Kirera 2003; M'Kirera and Ungar 2003). These taxa were chosen for analysis because of the modest degree to which they differ in the material properties of the foods they consume. At sites where the two taxa are sympatric, such as Lopé, Gabon, Central African chimpanzees and western lowland gorillas overlap considerably in their diets, preferring soft, succulent fruits. The two taxa do differ though, especially at times of fruit scarcity. At such times, gorillas fall back more on tough, fibrous foods than do chimpanzees (Tutin et al. 1991; Remis 1997). Average annual food type

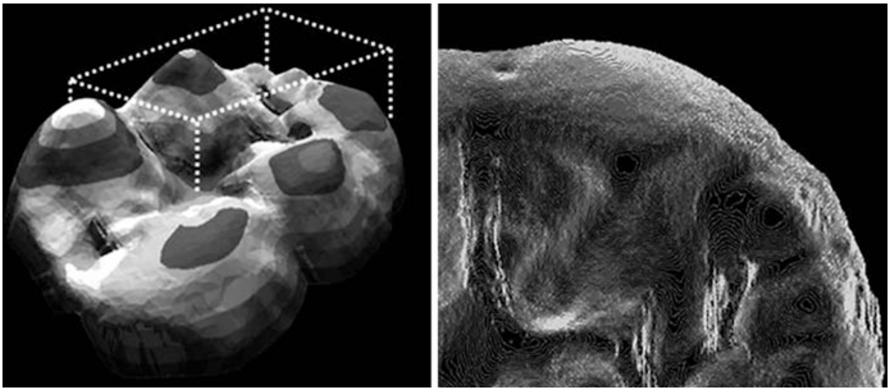


Fig. 1 Digital elevation model (*left*) and contour map (*right*) of a tooth. The contour interval is 25.4 μm, with a field of view corresponding to the area represented by the *box*

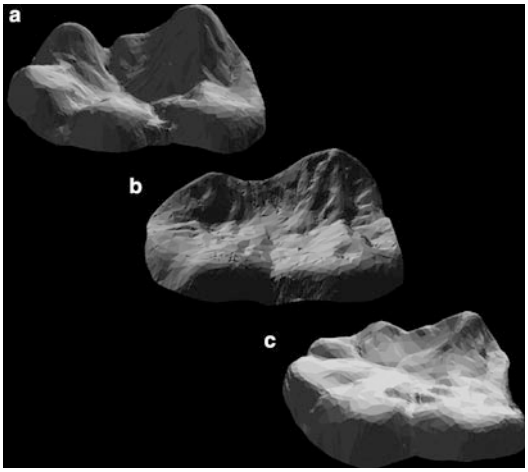
proportions reported for Central African common chimpanzees include about 70–80 % fruit flesh, as compared with 45–55 % fruit flesh for western lowland gorillas (Williamson et al. 1990; Kuroda 1992; Nishihara 1992; Tutin et al. 1997).

Dental topographic analysis of *Pongo pygmaeus pygmaeus* (Ungar and Taylor 2005) can add further insights into great ape molar form and function. Bornean orangutans consume an enormous variety of foods ranging from hard-husked, brittle nuts to soft fruits, to leaves, bark, and insects (MacKinnon 1977; Rodman 1977; Leighton 1993). While items consumed depend greatly on seasonal availability, average annual fruit to leaf proportions for *Pongo pygmaeus pygmaeus* are intermediate between those reported for *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*, with an average fruit percentage of about 55–65 % reported for the orangutans (MacKinnon 1977; Rodman 1977) – noting caveats concerning differences in data collection methods (Doran et al. 2002).

Data on average surface slope and occlusal relief are illustrated in Figs. 2, 3, and 4. These data are based on variably worn M_2s of *Pongo pygmaeus pygmaeus* ($n = 51$), *Pan troglodytes troglodytes* ($n = 54$), and *Gorilla gorilla gorilla* ($n = 47$). Methods of data collection are presented in detail elsewhere (Ungar and Williamson 2000; M'Kirera and Ungar 2003; Ungar and M'Kirera 2003). Occlusal surfaces were scanned as point clouds with lateral and vertical resolutions of 25.4 μm using a laser scanner. Resulting data files were opened as tables in ArcView 3.2 (ESRI Corp) Geographic Information Systems software, and digital elevation models were cropped to exclude areas below the lowest point of the occlusal basin. Average slope between adjacent points (surface slope) and the ratio of 3D to 2D planimetric area (occlusal relief) were then recorded for each specimen.

Results are illustrated in Figs. 2, 3, and 4. The species overlapped in three wear stages (as defined in Ungar 2004). As expected, more worn molar surfaces of each taxon showed less occlusal relief and shallower slopes. At any given stage of wear, however, gorillas had the steepest slopes and most occlusal relief, followed by orangutans. Chimpanzees had the shallowest molar cusps and least occlusal relief.

Fig. 2 Triangulated irregular network representations of surface data for M_2s of representative specimens at wear stage 1 (corresponding to Scott scores 10–14 (Scott 1979)): (**a**) *Gorilla gorilla gorilla* (CMNH B1781), (**b**) *Pongo pygmaeus pygmaeus* (SAPM 1981/62)



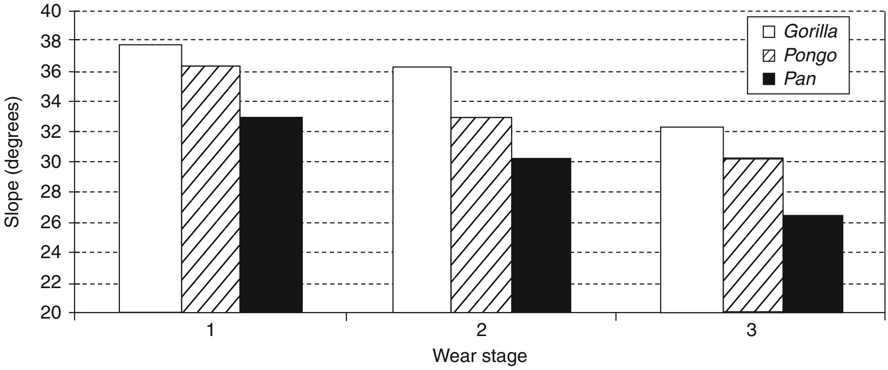


Fig. 3 Comparisons of mean surface slope values for given wear stages. Wear stages correspond to Scott wear scores as follows: (*1*) 10–14, (*2*) 15–19, (*3*) 20–24 (Scott 1979)

This example suggests several things. First, tooth shape changes with wear. As teeth wear down, cusp slopes and occlusal relief both decline. Such changes likely affect functional efficiency, and once teeth lose enough enamel, they essentially become dysfunctional (King et al. 2005). Further, apes with varying diets differ in the shapes of their teeth in ways that reflect the mechanical properties of foods that they eat. Species adapted to shearing and slicing tough leaves should have more occlusal relief and steeper sloped cusps than those adapted to crushing and grinding fruit. Cusp slope and occlusal relief values do mirror leaf-to-fruit ratios quite nicely for the great apes.

Another important point to come from this example is the notion that differences between species are of the same magnitude at different stages of wear. In fact, two-factor ANOVA results show no significant interaction between species and

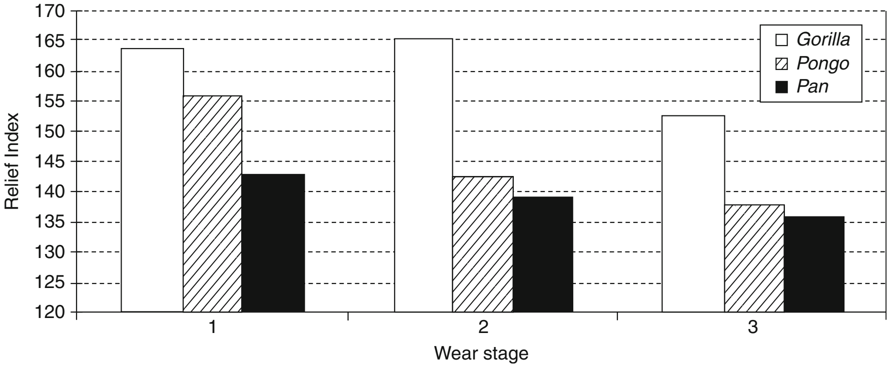


Fig. 4 Comparisons of mean surface occlusal relief values for given wear stages. Wear stages correspond to Scott wear scores as follows: (*1*) 10–14, (*2*) 15–19, (*3*) 20–24 (Scott 1979)

wear stage for any of the variables examined (M'Kirera and Ungar 2003; Ungar and M'Kirera 2003; Ungar 2004; Ungar and Taylor 2005; see also Klukkert et al. 2012). This basically means that differences between species remain consistent through the wear sequence. In other words, chimps, gorillas, and orangutans can be compared at any given wear stage and yield the same results, at least until very late in the game when teeth approach senescence, or their functional death (see King et al. 2005). This is important because it means that species need not be represented by unworn teeth as long as there is a baseline of comparative data for specimens with similar degrees of wear. This will allow reconstructions of diet for a whole new assortment of fossil taxa that could not be analyzed in the past for lack of available methods.

Fallback Foods and Dental Functional Morphology

As noted above, apes have a penchant for succulent, sugar-rich foods, a legacy of the ancestral catarrhine dietary adaptation (Ross 2000; Milton 2002; Ungar 2005). Differences in diet between catarrhines often rest largely with the seasonal shift to fallback foods taken when preferred resources are less available (e.g. Rogers et al. 1992; Lambert et al. 2004). In these cases, preferred resources are easy to digest, offer a low cost-benefit ratio, and may not result in selective pressures that would tax functional morphology. On the other hand, less desirable but seasonally critical fallback foods might require some morphological specialization (Robinson and Wilson 1998). This is not a new idea. Kinzey (1978), for example, noted that while *Callicebus moloch* and *C. torquatus* are both primarily frugivorous, the former evince longer shearing crests for slicing leaves and the latter have larger talonid basins for crushing insect chitin. He reasoned that dental morphology therefore reflects adaptations not only to primary foods but also to less frequently eaten but still critical ones.

As a result, gross differences in dental functional morphology need not relate to gross differences in preferred foods. Gorillas and chimpanzees at Lopé, for example, eat similar fruits much of the year (Williamson et al. 1990; Tutin and Fernandez 1993) but diverge at "crunch times" when preferred fruits are scarce. At such times, gorillas fall back more on leaves and other fibrous plant parts. The same is true for sympatric mountain gorillas and chimpanzees at the Bwindi Impenetrable National Park in Uganda (Stanford and Nkurunungi 2003). Differences between gorilla and chimpanzee occlusal morphology described here might then reflect fallback food choice more than everyday dietary preferences per se.

Function and Phylogeny

As indicated earlier, in discussions of tooth size, another issue to consider when inferring dietary adaptations from morphology is the effect of phylogeny. Phylogenetic inertia or baggage plays an important role in how adaptations manifest themselves (Kay and Ungar 1997). For example, while shearing quotients track diet within cercopithecoids, hominoids, and platyrrhines (with folivores having longer crests than frugivores within each of these higher-level taxa), cercopithecoids have relatively longer shearing crests than hominoids, and hominoids have relatively longer shearing crests than platyrrhines *independent of diet* (Kay and Covert 1984).

Because phylogeny determines the starting point for morphology, care must be taken when considering an extant baseline series to which an extinct species should be compared. Clearly, the choice of traits, out-groups, and methodology can all have a significant influence on the outcome of any analysis (e.g., Collard and Wood 2000; Lockwood et al. 2004; Strait and Grine 2004; Bjarnason et al. 2011). However, when all is said and done, early Miocene apes tend to have less well-developed shearing crests than do extant hominoids – though their ranges of SQ values are similar. It appears as if the extant hominoid range is upshifted relative to the early Miocene ape range but reflects a comparable array of diets (Kay and Ungar 1997; Ungar et al. 2004). This can be confirmed by "anchoring" the range using independent data, such as dental microwear patterning.

Dental Microwear Analyses

Investigators have known they could gain insights into jaw movement and tooth use through light microscope analyses of wear patterns on teeth for nearly a century (Simpson 1926; Butler 1952; Dahlberg 1960; Dahlberg and Kinzey 1962). Subsequent work rekindled interest in the topic (Grine 1977; Rensberger 1978; Walker et al. 1978; Puech and Prone 1979; Ryan 1979), as many workers shifted to using the scanning electron microscope. Since then, analyses of modern and fossil material have yielded insights into dietary variations within and between species and also new perspectives on the evolution of tooth use and diet in animals ranging from dinosaurs to human ancestors (see Teaford 1994; Rose and Ungar 1998; and Ungar 2002 for reviews).

The advantage of dental microwear analysis is that it provides evidence of what an animal was actually *doing* during its lifetime, not merely what it was capable of doing. The disadvantage, of course, is that it begins to document variations in diet in all its complexity. Thus, data samples of museum material need to include either exceptionally well-provenienced material or extremely large samples, and there needs to be some control, or awareness, of habitat differences between collection sites. Unfortunately, initial analyses of modern hominoids were generally based on small sample sizes (Gordon 1982, 1984; Teaford and Walker 1984; Teaford 1988; King et al. 1999), a factor which cannot be ignored when considering microwear data for animals, like chimpanzees and orangutans, with variable diets. Also, the earliest quantitative studies involved digitization of features on SEM images, a technique that has a subjective component that may complicate comparisons of results between different investigators (Grine et al. 2002). Still, initial results suggested diets dominated by soft fruit for the chimpanzee; fruit with perhaps some hard objects for the orangutan; and tough, leafy vegetation for the mountain gorilla (Teaford and Walker 1984; Teaford 1988) (see Fig. 5). Interestingly, comparisons of results for lowland and mountain gorillas yield microwear differences suggestive of the dietary differences documented in the literature (Tutin and Fernandez 1993; Remis 1997), with lowland gorillas showing a higher incidence of pitting on their molars as compared with mountain gorillas (King et al. 1999) (see Fig. 6).

As with studies of tooth morphology, dental microwear analyses have recently benefitted from a change to high-resolution 3D imaging and more sophisticated analyses (e.g., Ungar et al. 2003; Merceron et al. 2005; Scott et al. 2005, 2006). This has allowed more objective analyses of far larger samples, with the net result that populations of species are now being compared for intraspecific patterns of microwear and dental function (e.g., Krueger and Ungar 2010; Merceron et al. 2010; Daegling et al. 2011), and interspecific comparisons are now beginning to document the true range of microwear variation within taxa and between habitats. For African apes, however, the net result is perhaps not as clear as one would like. This is still probably due, in part, to a reliance on a relatively small, poorly provenienced sample, for even the most thorough recent studies of primate dental microwear (Calandra et al. 2012; Scott et al. 2012) have included samples of less than 20 specimens each of *Gorilla gorilla*, *G. beringei*, and *Pan troglodytes*. Thus, some results are what might be expected given what is known about African ape diets. For instance, the chimpanzee tends to clump together with known primate frugivores (Calandra et al. 2012; Scott et al. 2012). However, while *G. gorilla* was recognized as a consumer of abrasive plants in one study (Calandra et al. 2012), the addition of *G. beringei* to the other analysis introduced enough variation into the "gorilla" sample to make simple comparisons between genera more complicated (Scott et al. 2012). The net result is that, while there are suggestions of differences between *G. gorilla* and *G. beringei*, more work there is clearly necessary, and comparisons of *P. paniscus* with the other African apes are still lacking.

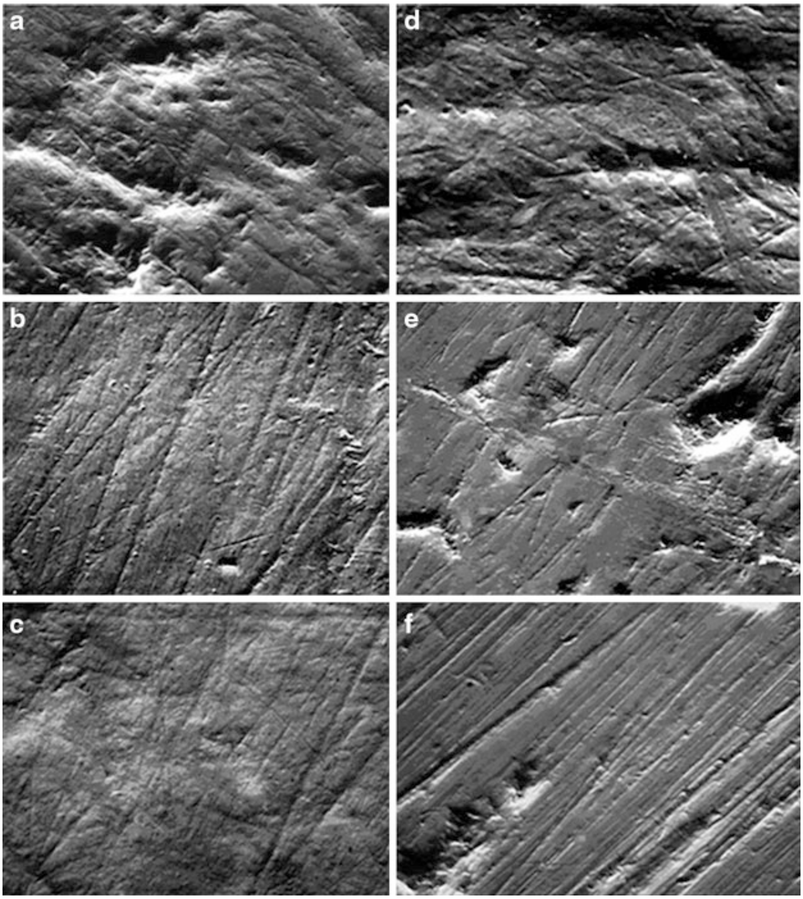


Fig. 5 Scanning electron micrographs of modern and fossil molars. (**a**) *Cebus apella*, (**b**) *Homo sapiens* (Arikara), (**c**) *Homo habilis*, (**d**) *Homo erectus*, (**e**) *Pan troglodytes*, (**f**) *Gorilla beringei*

As most studies of dental functional morphology hinge ultimately upon assumptions of the usefulness and selective advantage of the structures being measured, dental microwear analysis can certainly provide corroborative evidence for other hypotheses, for instance (as noted earlier), by "anchoring" analyses of dental morphological variation. Thus, dental microwear and molar shearing crest analyses for Eurasian fossil hominoids suggest that *Oreopithecus* was a folivore, *Ouranopithecus* was a hard-object feeder, and remaining forms such as *Dryopithecus* were soft-fruit eaters (Ungar et al. 2004; see also chapters "▶ Fossil Record of Miocene Hominoids," "▶ Hominoid Cranial Diversity and Adaptation," Vol. 2 and "▶ Potential Hominoid Ancestors for Hominidae," Vol. 3). By contrast, molar shearing crest analyses of African Miocene hominoids suggest at first glance that all were either soft-fruit eaters or hard-object feeders. However, the microwear evidence suggests that molar shearing quotients for the African Miocene taxa are

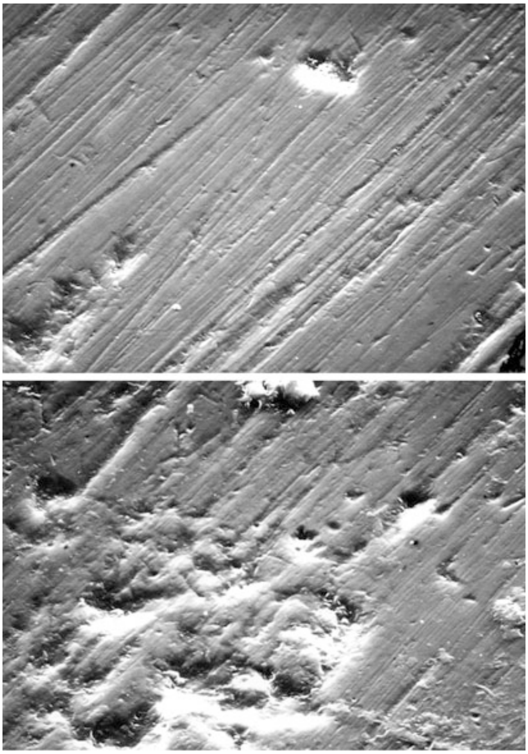


Fig. 6 Scanning electron micrographs of *Gorilla beringei* (*top*) and *Gorilla gorilla* (*bottom*)

"downshifted" by about 50 %, with *Rangwapithecus* as a folivore and the remaining taxa as soft-fruit eaters. This is exactly the same sort of shift we see comparing New World and Old World monkeys.

Obviously, given current knowledge about primate diets, dietary categorizations such as these are gross oversimplifications. Either fallback foods or preferred foods may be of crucial importance for the survival and reproduction of individuals. Thus, either may be a selective force to be reckoned with in the evolution of morphological differences. So how can they be teased apart? The key lies in the collaborative use of as many lines of evidence as possible, on samples that are as large as possible (Teaford et al. 1996; Teaford 2007). Of course, the fossil record will always be the ultimate arbiter of sample sizes in such analyses. Still, the combination of dental microwear analyses and other paleobiological data has allowed researchers to gain new perspectives on the dietary capabilities of the earliest hominins (Ungar et al. 2008; Grine et al. 2012). This has then spawned ongoing discussions about the proximate and ultimate causes of morphological differences among early hominins (Strait et al. 2009, 2013; Grine et al. 2012; Daegling et al. 2013), including, once again, insights into the distinction between dental *capabilities* and dental *use*, and also discussions of the ecological significance of observed differences in dental microwear (Daegling et al. 2013; Strait et al. 2013; Teaford et al. 2013). The bottom line is that researchers have only begun to tap into a wealth of data from innumerable sources ranging from laser scanning and dental microtextures to finite element modeling and nanoindentation. Through techniques such as these, researchers cannot help but gain a better grasp of variations in modern animals, and from that a better understanding of the intricacies of dental function, and a clearer picture of the past.

Conclusion

We live in an age of explosive technological advancement. Virtually every year, new techniques are used to answer new questions. The study of teeth has been but one small beneficiary of this phenomenon as recent advances in data collection and analysis are constantly being applied in new ways to studies of dental microstructure and development, tooth size and shape, and dental wear. This work is changing our perspectives on the lives and life histories of modern apes and human ancestors.

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Evolution of the Primate Brain

Dean Falk

Contents

Abstract

The active intelligence of today's primates flowered from trends that sculpted primate brain evolution across deep time: an increase in absolute brain size but a decrease in relative brain size (RBS, the ratio of brain size to body size) in bigger-bodied compared to smaller-bodied species (reflecting developmental scaling within species), increased RBS in highly "encephalized" species, and increased complexity of brain organization in conjunction with major adaptive shifts and selection for neurological specializations. Indices that quantify encephalization are discussed, as are developmental and physiological factors that constrain brain size. Data are provided which suggest that absolute brain size and RBS increased steadily rather than erratically during the last 3 Ma of hominin evolution, and the "received wisdom" that human frontal lobes are disproportionately enlarged is questioned. Despite the enormous importance

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D. Falk (✉)
Department of Anthropology, Florida State University, Tallahassee, FL, USA

School for Advanced Research, Santa Fe, NM, USA
e-mail: dfalk@fsu.edu; falk@sarsf.org

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attributed to the evolution of primate brain size, the conviction remains that size alone is not enough to account for the observed diversity in primate behavior and that circuitry, neurochemistry, and subsystems (modules) were reorganized within brains to accommodate evolving behavioral repertoires (such as those entailed in language). Arguments about the relative evolutionary merits of brain size versus neurological reorganization are reviewed and, to some extent, reconciled.

Introduction

The mammalian order Primates is known for a variety of species that are lively, curious, social, and intelligent. Nonhuman primates are of special interest to people not only because they are appealing and entertaining to watch but also because certain species (e.g., of macaques or baboons) are genetically close to humans, which makes them excellent animal models for medical research. As curious primates ourselves, we wonder about our evolutionary origins. One way to address this topic is to study and compare species from living primates that are thought to approximate broad stages (or grades) that occurred during some 65 Ma of primate evolution. Thus, one may compare particular anatomical structures or behaviors across appropriate representatives from the series prosimian → monkey → ape → human. When possible, such a *comparative method* should be supplemented with the *direct method* of studying fossil primates, which adds elements of specificity and time to the picture.

Within this broader context, we are also interested in the more specific question of how humans came to be not only the largest-brained primate but also the most intelligent species on Earth. In order to address this question, one must study primate brain evolution. From our general understanding of primate evolution, we know that certain major adaptations occurred in some groups and that these changed and sculpted evolving brains during many millions of years. For example, the anthropoid ancestors of living monkeys, apes, and humans became diurnal, and this shift from night living to day living dramatically impacted the lives and nervous systems of their descendants forever after. Thus, brains of diurnal primates have relatively enhanced visual compared to olfactory “modules.” Another broad shift that greatly impacted the nervous system occurred when very early primates shifted from primarily ground living to living in trees. This newfound arboreal life underscored the adaptive value of keen vision with depth perception and also led to improvements in sensory/motor coordination in conjunction with a variety of locomotor patterns that evolved in different arboreal species. More recently, some of these species shifted back to terrestrial living; and this, too, left its imprint on their nervous systems.

As with many groups of mammals (Jerison 1973; Radinsky 1979), relative brain size (RBS, the ratio of brain to body size) increased during the course of primate evolution. Some years ago, Radinsky (1979, p. 24) noted that “elucidation of the factors responsible for the widespread evolutionary trend of increase in RBS in mammals, and for the extreme to which that trend was carried in humans, remains a fascinating unsolved problem." Even before Radinsky's observation, Jerison was pondering the laws that governed the evolutionary increase in brain size for various groups of primates (and other animals) and partitioning the respective total increases into two parts: those associated with allometric scaling expected for given body sizes and any remaining increases (or decreases) in brain size, known as "residuals." Other workers, most notably Holloway (1974, 1979), emphasized the evolutionary importance of neurological reorganization that alters the quantitative relationships between brain nuclei, fiber tracts, and neuroreceptor sites (Holloway et al. 2004), thus allowing for rewired and altered neurochemistry in brains of similar (or different) size. Although the debate about the respective importance of brain size versus neurological reorganization is a false dichotomy (Gould 2001) (both are important, of course), it continues today (Falk and Gibson 2001). Bringing welcome balance, Holloway et al. (2004) note that the concept of reorganization in brain evolution is of less concern when one is examining broad genetic and evolutionary conservatism between large numbers of taxa (Jerison 1973; Finlay and Darlington 1995; Finlay et al. 2001; Kaskan and Finlay 2001), but more important when one attempts to explain species-specific differences in behavior (Preuss 2001; Holloway et al. 2004).

General Methods for Studying Primate Brain Evolution

The *direct method* of studying fossilized braincases and casts of their interiors (endocranial casts or endocasts) is the bread and butter of paleoneurology (literally "old" neurology). Cranial capacities that approximate brain volume in cm^3 (and also brain mass in grams) may be measured from skulls by traditional methods such as filling braincases with mustard seed that is then measured in a graduated cylinder or by obtaining volumes electronically from braincases (skulls) that have been subjected to three-dimensional computed tomography (3DCT). Indeed, because 3DCT is able to resolve small density differences, such as those between fossilized bone and attached rock matrix, it is particularly good for investigating fossils (Spoor et al. 2000) and has become useful as a noninvasive method for visualizing "virtual endocasts," e.g., by flood-filling the virtual braincase (Falk 2004b). Although brain size is actually slightly smaller than cranial capacity because of the fluids, vessels, and brain coverings (meninges) that occupy the braincase along with brain tissue, the difference is insignificant compared to other sources of intraspecific variation in brain size (according to Hofman (1983), cranial capacity = 1.05 brain size), and the two variables are frequently used interchangeably. An advantage of using cranial capacities across the board in comparative studies is that, unlike actual brains, cranial capacities may readily be obtained from available skulls of fossil and extant primates.

Endocasts sometimes occur naturally under propitious geological conditions (such as those that exist in parts of South Africa) or they may be prepared artificially from skulls using liquid latex (see Falk (1986) for details). Over the past 20 years, the use of 3DCT data for reconstructing and measuring virtual endocasts has undergone numerous validation studies (Conroy and Vannier 1985; Conroy et al. 1990, 1998; Spoor et al. 2000) and is rapidly becoming a preferred method (Falk 2004b). Physical endocasts may be measured to determine cranial capacity, e.g., by displacing them in water (see Holloway et al. (2004) for details), and as noted, the volumes of virtual endocasts may be measured electronically. Additionally, both kinds of endocasts (depending on their quality) may reveal positions of vessels and cranial nerves; details of suture closure, venous sinuses, and emissary veins (foramina); information about cortical asymmetries including brain shape (petalia) patterns; and information about sulcal patterns. Curiously, the most detailed endocasts are produced from skulls of relatively young individuals within a species (Connolly 1950) and from skulls of smaller-brained species within a group of related species (Radinsky 1972). The former may relate to the timing of suture closure during development, while the latter may explain why some of the South African australopithecine natural endocasts reproduce a good bit of detail (Falk 1980a, b).

By comparison, those using the *indirect method* of comparing neuroanatomical structures among living species have a veritable arsenal of methods at their disposal. Specific cortical areas may be investigated using currently available histochemical and immunocytochemical techniques (Preuss 2001; Sherwood et al. 2008), in addition to relying on classic cytoarchitectural studies (Amunts et al. 1999). Questions can therefore be asked about the types, sizes, density, distribution, and connections pertaining to individual neurons, cell columns, or layers of the cerebral cortex (within and across particular regions). The comparative neuroscientist is able to ponder whether or not (and how) additional cortical areas have been “added” during primate evolution and the extent to which they might be associated with enlarged brains (Felleman and Van Essen 1991; Preuss and Goldman-Rakic 1991; Sherwood et al. 2008). Whereas CT is ideal for imaging fossil material, magnetic resonance imaging (MRI) is more suitable for imaging the soft tissue structures that comparative neuroscientists study and may be performed noninvasively and in vivo. (Instead of relying on an X-ray source, MRI uses pulses of radiofrequency energy to map specimens that have been subjected to a strong magnetic field.) Even better, positron emission tomography (PET) and functional MRI (fMRI) are now commonly used to study functional processing in living human brains, and these techniques are beginning to be applied to nonhuman primates (Semendeferi 2001).

Although the increasingly sophisticated information gleaned from comparative brain studies is indispensable for interpreting paleoneurological data, the logistics of synthesizing findings from the *direct* and *indirect methods* for studying primate brain evolution remain tricky.

Structural, functional, and developmental disciplinary approaches have started to coalesce whereby brain structures can be seen developing and functioning through the many new noninvasive imaging techniques that are available today (Hofman and Falk 2012). All this allows better understanding not only of how the brain works in terms of movement and sensation but also of how it functions during sleep, during preparation for action, during thinking, and during emotions. These lines of investigation, which have major implications for normal as well as diseased human brain function, employ more and more complex methods and reveal the workings of smaller and smaller brain components. Consequently, the logistical problems of carrying out such studies in an evolutionary perspective and timescale loom ever larger (Oxnard 2004, pp. 1128–1129).

Quantifying Primate Brain Size

Certain allometric factors govern the general external and internal morphology of primate brains. Larger primate (indeed, mammalian) brains are characterized by more convolutions (gyri and sulci) than smaller ones (Radinsky 1975), which appears to be a mechanism for maintaining the ratio of surface (cortex) area to brain volume as brains enlarge (Falk 1980b; Jerison 1982). (This is not to say that sulci and convolutions are never associated nonallometrically with specialized features. Sometimes they are (Falk 1982), e.g., brains of prehensile-tailed New World monkeys have tail representations that are delimited by special sulci.) Neuronal density decreases with increased brain size, although mean neuronal size does not appear to scale allometrically with brain volume (Haug 1987). Compared to other mammals, the primate cerebral cortex is thicker and its layer IV is highly granulated (Haug 1987). The volume of gray matter is basically a linear function of brain volume, whereas the mass of interconnections that form the underlying white matter increases disproportionately with brain size (Ringo 1991; Hofman 2001). Curiously, women have relatively more gray matter than men (Haug 1987, see Falk (2001) for details regarding sexual dimorphism in primate brains).

Absolute brain size is hugely variable across living primates. Cranial capacities of living prosimians, monkeys, and gibbons overlap and together range between 1 and 205 cm^3, which is separate from the great ape range of 275–752 cm^3 (Falk 1986) (Fig. 1). The human range is above that for great apes and extends from around ~1,100 to 1,700 cm^3, excluding extreme outliers for purposes of comparison. But there is a problem here. The world's smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*), has a body weight of approximately 30 g (~1 oz), so how can we possibly compare its tiny brain size to those of larger primates such as the great apes? Clearly, a more meaningful parameter would be the ratio between brain size and body size, known as RBS. However, RBS is itself confounded by certain very powerful allometric scaling constraints that apply ontogenetically as individuals develop from smaller-bodied babies to adults (Passingham 1975b) and in interspecific comparisons of smaller-bodied with larger-bodied primates (Schultz 1956) (Fig. 2). Allometric scaling is why human babies appear to have relatively big heads (brains) compared to adults despite the fact that their absolute brain sizes are smaller, and it is why we should not be particularly impressed by the fact that little squirrel monkeys have an average RBS of about 0.02, which is equivalent to that of humans (Falk and Dudek 1993).

In order to "subtract" the effects of allometric scaling, comparative studies of primate brain size have traditionally relied on quotients that express "residual"

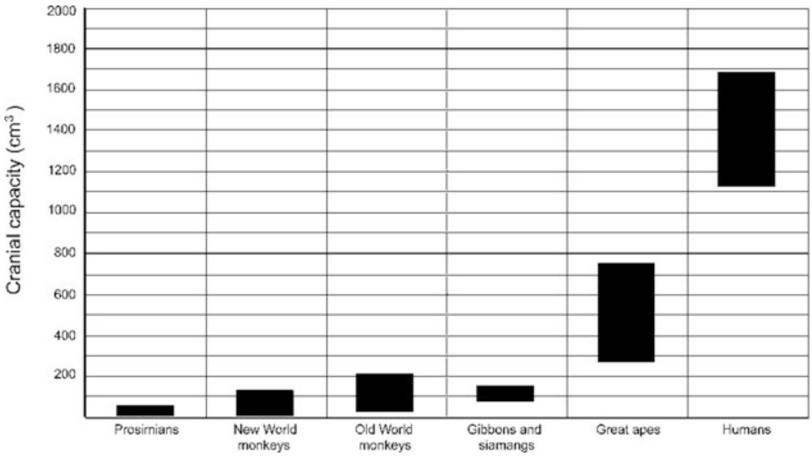

Fig. 1 Ranges of cranial capacities in living primates, excluding far-reaching extremes in humans for comparative purposes (Modified from Falk 1986)

factors after the effects of body size have been removed from paleoneurological data (Falk 1980b). Thus, Bauchot and Stephan (1966, 1969) and Stephan (1972) developed the index of progression (IP) by using brain weight/body weight data from basal insectivores and calculating the regression equation:

$$\log\ h = 1.632 + 0.63\ \log\ k \tag{1}$$

where h = brain weight and k = body weight. From this equation, "basal" brain weight (BG) can be predicted for a given primate species by substituting its mean body weight into the equation. The ratio between actual mean brain weight of the species (progressive size = PrG) and the predicted "basal size" (BG) equals IP, the index of progression,

$$\mathrm{IP} = \frac{\mathrm{PrG}}{\mathrm{BG}} \tag{2}$$

Jerison's (1973) famous encephalization quotient (EQ) is similar but uses brain weight/body weight data from living mammals rather than insectivores to establish the baseline regression and resulting classic formula:

$$\mathrm{EQ} = \frac{E_i}{0.12P_i^{67}} \tag{3}$$

where E_i = actual brain size and P_i = predicted brain size.

(Like other workers (Martin 1982, 1990), Jerison (2001) now uses a regression equation with an exponent of 0.75, instead of 0.67.) It should be noted, however, that the comparative results of EQ studies depend very much on the group selected for the baseline data (Holloway and Post 1982) and that there is an artifactual

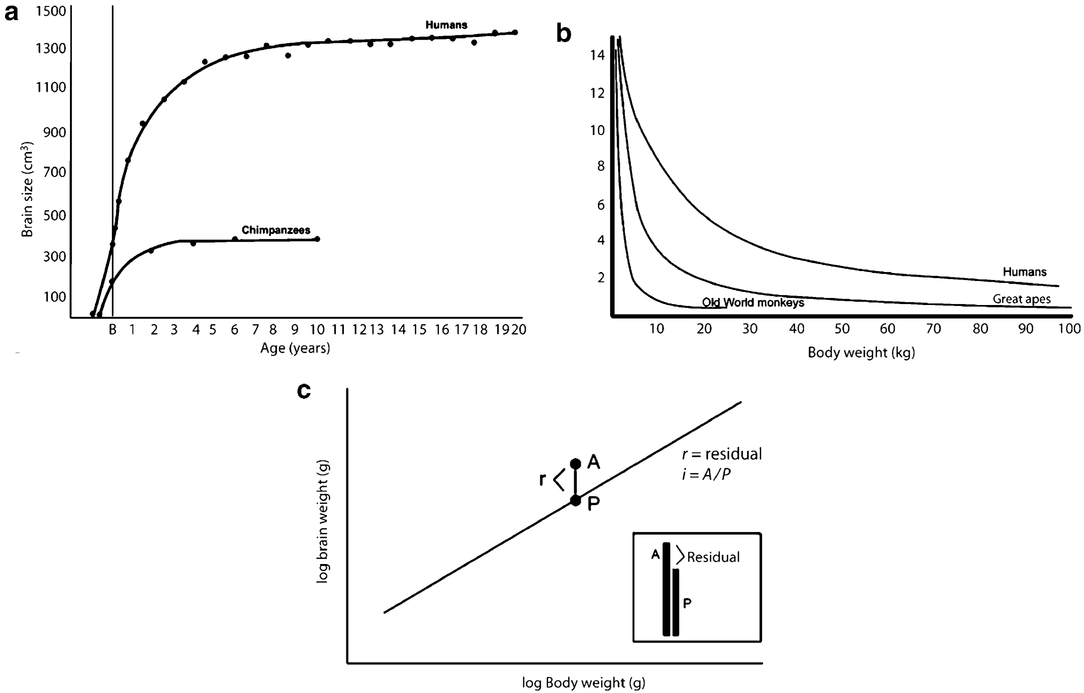

Fig. 2 Brain size and relative brain size (RBS) in humans and other primates. (**a**) Brain size growth in humans and chimpanzees. Brain growth in humans is at a higher rate after birth (**b**), which results in larger cranial capacities (and brain masses) for humans than chimpanzees at any given age (or body weight) (Modified after Passingham 1975b). (**b**) Relative brain size (RBS, brain size/body size) plotted against body weight for humans, great apes, and Old World monkeys. The shapes of these curves are inverse to those above (in (**a**)) and, again, are stacked because of different rates of postnatal brain growth in the three groups. At any given body weight (and age), humans have RBS above those of apes, which are above those of monkeys. At smaller body weights (and therefore ages), primates have greater RBS (which is why human infants appear to have big heads) (Modified from Schultz 1956). (**c**) Simple schematic that illustrates indices of relative

tendency for encephalization to be overestimated for smaller-bodied species but underestimated for larger ones (Radinsky 1982). One may also utilize similar regressions to estimate residual numbers of extra neurons (Jerison's extra neuron index, Nc) or to determine how "encephalized" particular parts of the brain are. Toward these ends, Stephan et al.'s (1970) widely cited data for primate brains have been a gold mine for evolutionary studies.

The Evolution of Primate Brain Size

Compared to basal insectivores, primates evolved enlarged brain size/body size ratios (Radinsky 1975). Cranial capacity estimates for a dozen available Eocene and Oligocene prosimian skulls are all under 11 cm^3, and their EQs suggest that the Eocene adapiforms *Smilodectes*, *Adapis*, and *Notharctus* were relatively smaller-brained than modern prosimians and those for Tarsiiformes (for which there is a brief series) increased through time (Radinsky 1975; Gurche 1982). By about 45 Ma, some prosimians appear to have RBS at the lower end of modern ranges (Radinsky 1975). Radinsky (1974) noted that an Oligocene anthropoid, *Aegyptopithecus*, had a cranial capacity of approximately 32 cm^3 but had nevertheless attained an anthropoid level of RBS. The Miocene hominoid *Proconsul* had a comparatively whopping endocranial volume of 167 cm^3 and an estimated body weight of ~11 kg, giving it a relatively bigger brain than modern monkeys of comparable body size (Walker et al. 1983). Recent analyses confirm that selection for enlarged brains began early in primate evolution but also indicate that brain size decreased independently in certain branches of strepsirhines, New World monkeys, and Old World monkeys (Montgomery et al. 2010). Over a quarter of a century ago, Radinsky (1974) summarized his findings from the "scanty" fossil record of primate brain evolution by observing that increased RBS dramatically distinguishes human brains from those of other primates, and he further suggested that this increase occurred relatively recently, beginning no more than 4–5 Ma (Radinsky 1975).

Although most modern anthropoids have brains that are relatively larger than those of modern prosimians (Bauchot and Stephan 1969), caution must be exercised when using EQs or similar indices to assess cognitive capacities. Despite the fact that EQs correlate to some degree with primate feeding behaviors

Fig. 2 (continued) brain size (i), the names of which vary (EQ, IP) with the reference group for the linear regression. When transformed to logarithms, brain size versus body size data (such as those in (**a**)) have a linear relationship (the *straight line* or linear regression shown in (**c**)). *P* is the mean value for brain size predicted by the regression for a species at a given mean body weight; *A* is the actual mean value of brain size for that species. The index of RBS (or encephalization), *i*, is the ratio of *A* to *P*. The difference between *P* and *A*, the residual (*r*), is the extra (or reduced) mean brain size that a species has compared to a species of similar mean body size in the reference group. The reference group (be it composed of mammals, insectivores, or just monkeys) is very important for interpreting indices (frugivorous primates are more encephalized than folivorous ones (Jerison 1973; Clutton-Brock and Harvey 1980; Milton 1988) and nonhuman primates that are omnivorous extractive foragers generally have higher IPs than the others (Gibson 1986), such indices fail to predict relative cognitive capacities. Gibson (2001) argues persuasively that compared to monkeys, great apes possess greater mental constructional capacities and cognitive abilities in realms once thought to be uniquely human. Using a test for mental flexibility that separates apes from monkeys (the Transfer Index), she demonstrates that absolute brain size, body size, and extra neurons all correlate with performance, while EQ does not. Gibson therefore suggests that "the most practical measure for distinguishing intelligence and predicting the presence of humanlike mental skills in hominid fossils is absolute brain size" (Gibson 2001, p. 92). Other studies also emphasize absolute over RBS as the best predictor of advanced cognition. Thus, "Only in terms of absolute mass and the rate of change in absolute mass has the increase in brain size been exceptional along the terminal branch leading to humans. Once scaling effects with body mass have been accounted for the rate of increase in relative brain mass remains high but is not exceptional" (Montgomery et al. 2010, p. 11). Others reinforce this suggestion (Deaner et al. 2007; Herculano-Houzel 2009, 2012). For example, "the functional integration of different brain regions is so strong that the brain as a whole is a relevant unit for cognitive performance" (Deaner et al. 2007, p. 121), and "the most likely brain alteration resulting from selection for any behavioral ability may be a coordinated enlargement of the entire nonolfactory brain" (Finlay and Darlington 1995, p. 1578).

The relationship between primate brain size and cognition may also be explored by investigating the interaction between life-history adaptations, brain growth, and cognitive levels (primate cognitive ecology Garber (2004)). In one study, postnatal brain growth patterns were found to be highly variable among anthropoids (Leigh 2004). Leigh discerned two alternate life-history strategies that concern the metabolic costs of infant brain growth. In one, favored by Old World monkeys, relatively large-bodied mothers mature late and give birth to infants that require relatively little postnatal brain growth. This strategy requires high maternal metabolic investments during pregnancy. In the second strategy, exploited by tamarins, females mature especially early and produce offspring with brains that grow for a relatively long period of time during the postnatal period, which shifts some of their metabolic costs away from the mother and to others (including the offspring). Leigh notes that chimpanzees and humans are difficult to categorize in terms of these two strategies and adds that differences in patterns of brain growth should be viewed as part of a more general complex of life-history traits rather than as direct pacesetters of life histories. Citing comparative studies on the cognitive abilities of squirrel monkeys, tamarins, and baboons, Leigh concludes that life-history strategies may have coevolved with cognitive abilities in association with evolutionary changes in brain development.

Other studies investigate the perplexing question of how primates (including humans) were energetically able to grow relatively large brains that are metabolically "expensive" to maintain compared to the whole body. The maternal energy hypothesis (MEH) proposes that the mother's relative basal metabolic rate (BMR) during an infant's gestation determines its neonatal brain mass and that subsequent maternal investment while the infant is nutritionally dependent is also an important factor for developing big brains (Martin 1996). The MEH is sometimes contrasted with the expensive-tissue hypothesis (ETH), which proposes that relatively encephalized primates are able to maintain their brain's metabolic requirements because there has been an evolutionary trade-off in which brain tissue has increased at the expense (decrease in mass) of other metabolically expensive tissues such as guts, heart, liver, or kidney (Aiello and Wheeler 1995; Aiello et al. 2001). The two hypotheses should be viewed as complementary rather than contradictory because the MEH focuses on maternal energetics invested in offspring during gestation and lactation, while the ETH picks up from there by focusing on metabolic dynamics of brain growth and maintenance after weaning (Aiello et al. 2001). While the wider applicability of both hypotheses to mammals has been challenged by findings for bats (Jones and MacLarnon 2004), the recent trend toward studies that explore physiological and metabolic constraints on brain size and development is welcome and dovetails nicely with primate life-history studies. (Another constraint hypothesis about brain size evolution, the radiator hypothesis, concerns the evolution of vascular anatomy in response to brain temperature regulation combined with selection for bipedalism (Falk 1990, 2007)).

Parsing Brain Size Evolution

But what are the possible neurological correlates of increased brain size during primate evolution? To address this, Finlay and colleagues concentrated on critical factors that drove mammalian (including primate) brain size, especially the kinds and numbers of neurons generated during development (Finlay and Darlington 1995; Finlay et al. 2001). They found that the longer cytogenesis is prolonged for a given structure (based on timing of the peak in "neuronal birthdays"), the larger the structure will ultimately be. Since mammalian neurogenesis of brain parts proceeds uniformly (i.e., the order is conserved), "by far the most useful predictors of structure sizes are the sizes of other brain structures" (Finlay et al. 2001, p. 268). It should be noted, however, that olfactory bulbs (and medulla) are an exception to this rule because they are smaller overall in anthropoids than prosimians and may map onto nocturnal versus diurnal niches (Barton et al. 1995). A result of this regularity is that most parts of mammalian brains enlarged together, which led Finlay et al. to suggest that enlarged isocortices could have been by-products of structural developmental constraints (spandrels) that were only later co-opted for specific functions. The suggestion that the sizes of different brain structures are a consequence of overall brain size has been the subject of more controversy than it should have (Barton and Harvey 2000; Barton 2001; Oxnard 2004), because the Finlay et al. model in fact accommodates independent variation of individual brain parts that may be associated with specific behavioral advantages (e.g., foraging ability). Generally, this latter type of brain growth, which makes up the unaccounted-for variance in Finlay et al.'s (2001) model, underlies a small (but presumably evolutionarily important) variation of individual structure size on the order of two- to threefold.

Evolution of Brain Size in Hominins

As noted, cranial capacities may be obtained for fossil hominins by measuring their endocasts (actual or virtual). Error may be introduced, however, because fossil endocasts are rarely whole and, thus, usually require partial reconstruction. Because morphological differences were found to distinguish the frontal lobes and temporal poles of robust (*Paranthropus*) and gracile (*Australopithecus africanus*) australopithecines, new endocast reconstructions were provided for four *Paranthropus* specimens, which reduced the mean cranial capacity for the genus to the point where it approximated that of *A. africanus* (see Falk et al. (2000) for details). These cranial capacities and others appear in Table 1 and Fig. 3. (For more extensive data, the reader is referred to Appendix 1 of Holloway et al. (2004)).

A number of conclusions regarding the evolution of absolute brain size in hominins are suggested by Fig. 3. Although brain size remained conservative during the evolution of *Paranthropus*, it increased in *Australopithecus* and between the latter and specimens that lived more recently (~1.7–1.9 Ma) in Africa and the Republic of Georgia. The overall morphology of these more recent specimens is transitional enough so that some workers place them in *Australopithecus* while others include them in early *Homo* (Wood and Collard 1999; Balter and Gibbons 2002). If, indeed, these specimens are transitional, then the received wisdom that brain size suddenly "took off" in the genus *Homo* around 2.0 Ma needs serious reevaluation (Falk et al. 2000; Falk 2004b). Thus, rather than there being a jump in cranial capacity in early *Homo*, cranial capacity may have begun increasing in the *Australopithecus* ancestors of *Homo* a million years earlier (Falk et al. 2000). With the redating of Java sites (Swisher et al. 1994; Huffman 2001) pushing certain cranial capacities further into the past, there is no longer the discontinuity in the trend for increasing cranial capacity (Falk 1987b, 1998) that once contributed to the suggestion that brain size evolution underwent "punctuated" events (Hofman 1983; Leigh 1992; Ruff et al. 1997). Rather, the recent discovery of LB1, the small-brained type specimen for *Homo floresiensis* (Brown et al. 2004; Morwood et al. 2004), lends an entirely new perspective to the study of hominin brain size evolution (Falk et al. 2005): From australopithecines through extant *Homo*, upward selection widened the range of brain size variation, while australopithecine-sized brains may have continued to provide the lower boundary (at least, until very recently). Thus, to some extent, Fig. 3 encapsulates the interplay between selection for brain size (vertical vector) and selection for neurological reorganization (horizontal vector).

But what about the evolution of RBS in hominins? After all, LB1 was tiny, only about a meter in stature (Brown et al. 2004), which must certainly account for much of

Table 1 Cranial capacities for various adult hominins

Species	Date (Ma)	Specimen	Adult cm^3	Reference
Australopithecus				
A. afarensis	~3.2	AL 333-105	343	Falk (1987b)
–	~3.2	AL 162-28	375	Falk (1985)
A. africanus	~3.0	MLD 37/38	425	Conroy et al. (1990)
–	~2.75	Sts 60	400	Holloway et al. (2004)
–	–	Sts 71	428	Holloway et al. (2004)
–	–	Sts 5	485	Holloway et al. (2004)
–	–	Sts 19	436	Holloway et al. (2004)
–	–	Stw 505	515	Conroy et al. (1998)
Paranthropus				
P. aethiopicus	~2.5	KNM-WT 17000	410	Walker et al. (1986)
P. boisei	~2.4	Omo L339y-6	427	Holloway et al. (2004)
–	~1.9	KNM-ER 23000	491	Brown et al. (1993)
–	~1.8	KNM-WT 17400	400	Holloway et al. (2004)
–	~1.8	OH 5	500	Falk et al. (2000)
–	~1.9	KNM-ER 407	438	Falk et al. (2000)
–	~1.7	KNM-ER 732	466	Falk et al. (2000)
P. robustus	~1.7	SK 1585	476	Falk et al. (2000)
Australopithecus/Homo?				
–	~1.9	KNM-ER 1470	752	Holloway et al. (2004)
–	~1.75	D2700	600	Vekua et al. (2002)
–	–	D2282	650	Gabunia et al. (2000)
–	–	D2280	780	Gabunia et al. (2000)
Homo erectus				
Java (Sangiran)	~1.6	$n = 6$	Mean = 932	Holloway et al. (2004)
Africa	~1.5	KNM-WT 15000	909	Walker and Leakey (1993)
Java (Trinil)	~0.9	Trinil 2	940	Holloway et al. (2004)
China (Beijing)	~0.585	Skull D1	1,020	Weidenreich (1943)
China (Beijing)	~0.423	$n = 3$	Mean = 1,090	Weidenreich (1943)
Hexian	~0.412	–	1,025	Wu et al. (2005)
Java (Solo)	~0.027	$n = 6$	Mean = 1,149	Holloway et al. (2004)
Homo				
European	~0.2	–	Mean = 1,314	Hofman (1983)
Neanderthals	~0.07	–	Mean = 1,487	Hofman (1983)
European	~0.04	–	Mean = 1,460	Hofman (1983)

(*continued*)

Table 1 (continued)

Species	Date (Ma)	Specimen	Adult cm^3	Reference
H. sapiens	~0.01	–	Mean = 1,330	Holloway et al. (2004)
H. floresiensis	~0.018	LB1	417	Falk et al. (2005)

Following Holloway et al. (2004), the chronological data are approximate middle values of the ranges for estimated dates (see also Falk et al. 2000). See Fig. 3 for plots of data

the recent variation in brain size. Although many workers have estimated EQs for fossil hominins, these estimates must be taken with a grain of salt because of the difficulty of determining surrogates for body mass. Without an associated skull, how does one identify the species of postcrania such as femurs that are often used to predict body mass or stature? Needless to say, the few known hominin partial skeletons are extremely important in this endeavor. Conservatively, we know exactly this much about encephalization in hominins: living people have brains and (separately) neocortices that are approximately three times as large as expected for nonhuman primates of the same body size (Stephan et al. 1970; Passingham 1973, 1975a; Passingham and Ettlinger 1974), and, surprisingly, this is true using regression equations based on all nonhuman primates, just monkeys and apes, or just apes (Stephan 1972; Falk 1980b). Turning to the hominin fossil record, there are two skeletons that provide important data. First, there is the approximately 3′6″ Lucy (AL 288-1), dated to a bit over 3.0 Ma. Although a definitive cranial capacity could not be obtained from this specimen, hominin cranial capacities of less than 400 cm^3 occurred in other hominins from that time and place (Table 1), so it is safe to say that small-bodied australopithecines from Hadar, Ethiopia, had ape-sized body masses that were probably associated with ape-sized brains (giving them an RBS index of $i = 1$). Fast-forwarding to ~1.5 Ma, the *H. erectus* skeleton from Nariokotome, Kenya (KNM-WT 15000), paints quite a different picture. By the time he reached adulthood, it was projected that this “lad” would have reached a stature of over 6 f. and a cranial capacity of 909 cm^3 (Walker and Leakey 1993). That capacity is twice the means for both *A. africanus* and *Paranthropus* (Table 1) and roughly twice the means for living great apes (490 cm^3 for gorillas, 375 cm^3 for common chimpanzees and for orangutans (Falk 2000b), p. 312). It is also 2/3 of 1,364 cm^3, which is very close to the oft-cited world mean for contemporary *H. sapiens* of 1,350 cm^3. It therefore looks as if African *H. erectus* that lived ~1.5 Ma may have had a brain mass that was twice the size predicted for a living nonhuman primate of equivalent body mass ($i = 2$) or, put another way, that *H. erectus* was two-thirds as encephalized as *H. sapiens*. These few data provide nice 1-2-3 estimates for indices of RBS at ~3.0 Ma, ~1.5 Ma, and today (Fig. 3). Beyond this, conjecture about the past evolution of hominin encephalization remains just that.

One can, however, make reasoned inferences about future brain size evolution. In fascinating research, Hofman (2001, 2012) applied the design principles and

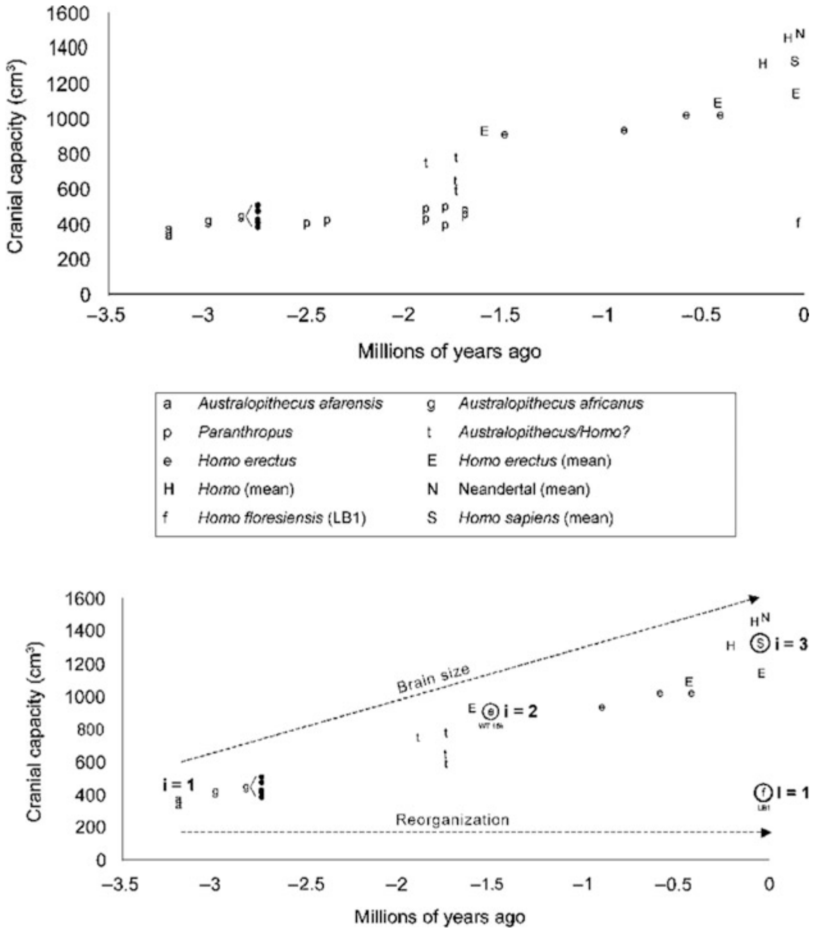

Fig. 3 Cranial capacities of select hominins plotted against time (Data from Table 1) (*Above*). Plot includes capacities for robust australopithecines (*Paranthropus*). The trend for brain size increase appears flat until around 2.0 Ma and then begins to increase in *Homo*. (*Below*). The same plot, but without the *Paranthropus* specimens (generally thought not to be ancestral to *Homo*). The trend toward brain size increase now appears to increase from before 3.0 Ma. Part of the reason for this is the recently described "transitional" specimens from Dmanisi, Republic of Georgia (listed under *Australopithecus*/*Homo* in Table 1). The earliest australopithecines and relatively recent LB1 (*H. floresiensis*) have brain sizes expected for apes of equivalent body sizes ($i = 1$), *H. erectus* from Nariokotome (KNM-WT 15000) has a brain that is twice the size expected for similarly sized apes ($i = 2$), and contemporary *H. sapiens*' mean brain size is three times that expected for apes of equivalent body size ($i = 3$). This figure illustrates the trends for increasing brain size (*vertical axis*) and ongoing neurological reorganization (*horizontal axis*)

operational modes (including energetic and neural processing constraints) that underlie information processing in primate brains to the task of modeling the limits of future brain size evolution in *H. sapiens*. His model predicts that as brain size increases beyond a certain critical point, subcortical volume (cerebellum, brain stem, diencephalon, etc.) will decrease in conjunction with increasing white matter. The net result would be that hominins with brains enlarged beyond that critical point would have a declining capability for neuronal integration despite an increased number of neurons. The critical point is ~3,500 cm^3, beyond which "any further step in the evolution of intelligence will then have to take place outside our nervous system, in a technological world where the selection mechanisms and forces are radically different from those operating in nature" (Hofman 2001 p. 125). Although Hofman's model does not incorporate anatomical constraints that govern head size and parturition, perhaps the technological world he envisions will, indeed, make it possible for women to bear (presumably) bigger-brained neonates.

The Evolution of Neurological Reorganization

Despite the enormous energy that paleoneurologists have devoted to studying primate brain size evolution, there remains a conviction that size alone is not enough to account for the observed diversity in primate behavior and that circuitry, neurochemistry, and subsystems (modules) must have become reorganized within brains to accommodate evolving behavioral repertoires (Preuss 2001; Holloway et al. 2004). Preuss, in fact, goes so far as to suggest that "the cortex is a veritable hotbed of evolutionary reorganization" (2001, p. 140). Although reorganization was undoubtedly important, deciphering the details of internal brain evolution is much more difficult than studying the gross phenomenon of brain size. Nevertheless, information yielded by both *direct* and *indirect methods* sheds some light on at least the broad aspects of neurological reorganization that occurred during primate evolution.

Comparisons of brains of basal insectivores and living primates suggest early evolutionary trends in primates that included not only the larger brain size/body size ratios noted above but also relatively enlarged neocortices for brain size, a decrease in the relative size of the olfactory bulbs, an increase in the amount of visual cortex, and development of a central sulcus in anthropoids rather than the coronal sulcus seen in prosimians (Radinsky 1975). At histological levels, layer 4 of the posterior cingulate cortex appears to be less densely packed with small cells in prosimians than anthropoids (Zilles et al. 1986), a finding that has now been extended to include much of the parietal and temporal cortices (Preuss and Goldman-Rakic 1991). The fossil record of prosimian endocasts helps to pin down the approximate dates when some of these primate specializations occurred (Radinsky 1974, 1975; Gurche 1982). Thus, visual and temporal cortices had expanded to comparable modern levels in some ancestral tarsiiform and lemuriform primates by ~55 Ma (Early Eocene), but frontal lobes were still relatively small except in the line leading to *Adapis* (Radinsky 1975; Gurche 1982). Analysis of the fossil record of anthropoid endocasts, particularly partial endocasts of *Aegyptopithecus*, reveals that by ~25–30 Ma (Oligocene), olfactory lobes had reduced and visual cortices had expanded compared to prosimians. Although its frontal lobes appeared to be small compared to modern anthropoids, *Aegyptopithecus* had an anthropoid-like central sulcus instead of a longitudinally oriented fissure, the coronal sulcus, which separates head from forelimb representations in primary somatosensory cortices of prosimians (Radinsky 1975). The oldest record of an anthropoid endocast of modern appearance is that of ~18 Ma *Proconsul* (Falk 1983; Walker et al. 1983). Regarding neurological reorganization during primate evolution, Radinsky (1974, p. 25) summarized:

> Since *Aegyptopithecus*, *Dolichocebus*, and *Apidium* are among the oldest known pongids, ceboids, and cercopithecoids, respectively, it is likely that elaborations of visual abilities and reduction of olfaction were among the features involved in the initial emergence of higher primates from prosimians. It is interesting that those same features, although not as extensively developed, appear to have been among the key adaptive features at the base of the great Eocene prosimian radiations.

A comparative study of endocasts from extant New and Old World monkeys describes various cortical specializations that were independently evolved in both groups as well as similarities that were retained from a common ancestor (Falk 1981). Within Old World monkeys, cercopithecine sulcal patterns appear to be more derived than colobines as manifested in relative expansion of prefrontal and inferior temporal integration cortices (Falk 1978). Radinsky (1974) showed that a cercopithecoid endocast from *Mesopithecus*, dated to ~9 Ma, exhibits the typical colobine pattern and is similar to the brain of ~6 Ma *Libypithecus*. Thus, the modern colobine sulcal pattern, which appears to represent the more primitive condition, had occurred by at least 9 Ma. He also noted that the derived cercopithecine sulcal pattern had appeared by ~2 Ma in *Paradolichopithecus*.

The addition of new cortical areas may have provided an opportunity for the evolution of new behavioral capacities (Kaas 1987, 1995; Kass and Preuss 2008; Allman 1990, 1977; Felleman and Van Essen 1991; Preuss and Goldman-Rakic 1991). To date, primates are known to possess 50–100 cortical areas, and it has been hypothesized that many of these may be higher-order areas that are unique such as dorsolateral prefrontal, posterior parietal, and inferotemporal cortices (Preuss 2001). Preuss also notes that higher-order association regions of primates are strongly connected with each other and these regions are all connected with a prominent thalamic structure, the medial pulvinar, which has no obvious counterpart in other mammals. He further suggests, “not only do primates possess primate-specific higher-order cortical territories, but these territories form a distinctive connectional system” (Preuss 2001, p. 153). The suggestion that new cortical areas constitute a natural by-product of increasing brain size is consistent with Ringo’s (1991) mechanistic observation that enlarging brains would become swamped with white matter without neurological reorganization that increased the number of local (as opposed to longer corticocortical) connections and therefore areas (Hofman 2001).

Relatively recent comparative work also suggests that the cerebellum, long known to be important for motor coordination and now thought to contribute to higher cognitive functions in humans (Fiez 1996; Muller et al. 1998; MacLeod 2012), underwent neurological reorganization during primate evolution. Thus, the lateral cerebellar system is relatively large in chimpanzees and gibbons, while a central nucleus (the dentate nucleus, the output of which influences the cerebral motor cortex) is larger in humans than apes (Matano et al. 1985; Matano and Hirasaki 1997). This is particularly interesting in light of the fact that the human cerebellum appears to be smaller than expected for an ape brain of human size (Semendeferi and Damasio 2000).

It is important to keep in mind that a part of the brain does not need to be "new" or grossly enlarged for reorganization to occur. For example, Armstrong et al. (1987) investigated which thalamic nuclei changed in volume relative to the rest of the thalamus and found that, after controlling for the size of the brain, anthropoids that lived in single-male societies had more anterior principal thalamic neurons than primates that lived in multimale societies. Since limbic structures are known to be important for social life, it is not surprising that the sizes and reorganizations of limbic structures may link more than those of other structures to specific behaviors and niches (e.g., the relationship of olfactory bulbs with nocturnal and diurnal niches) (Finlay et al. 2001). Along somewhat related lines but focusing on gross brain size rather than reorganization, the "social brain" [or Machiavellian intelligence] hypothesis incorporates data showing that neocortical size correlates with social group size and proposes that large primate brains evolved in response to living in complexly bonded social groups (Falk and Dudek 1993; Dunbar 1998, 2003; Byrne 2000).

While complex social life may indeed have contributed directly or indirectly to selection for large primate brains, partitioning the types of internal reorganization that characterize different groups hones in on other aspects of lifestyle. In a follow-up to Finlay et al.'s research, de Winter and Oxnard (2001) performed similar multivariate analyses on a greatly enlarged data set that confirmed earlier findings (Finlay and Darlington 1995) and extended earlier multivariate analyses to include a series of brain-part ratios that partly reflected input/output relationships within the brain. Rather than grouping primates according to phylogenetic relationships, however, the groups that emerged from the comparisons were based on similar lifestyles, such as lower-limb-dominated lifestyles that involve much leaping (tarsiers, indriids, galagos, mouse lemurs) and four-limb-dominated lifestyles (some strepsirhines, New and Old World monkeys) (de Winter and Oxnard 2001; Oxnard 2004). Genera with upper-limb-dominated lifestyles involving hand-feeding in arboreal habitats and escaping by upper-limb acrobatics (*Ateles*, *Lagothrix*, *Hylobates*, *Pan*, and *Gorilla*) also emerged as a cluster.

The brain organization that is involved in the trend along the axis toward the forelimb dominant species is increasing expansion of the neocortex, striatum, cerebellum, and diencephalon relative to medulla. This particular pattern of brain organization could involve brain functions based on expansion of higher levels of voluntary sensory and motor control. In turn, they could relate to a trend toward creatures with greater degrees of complex voluntary behavior and increased capacity to plan strategically and to control complex motor actions (Oxnard 2004, p. 1147).

Significantly, similar multivariate analyses separate humans from chimpanzees to a degree that rivals the extent of separation within all Old World monkeys and apes, which is not only contrary to the much-cited close genetic relationship between *Pan* and *Homo* but also implies that the internal organization of the human brain is quantitatively different from any other living primate (Oxnard 2004). Further, the differences between chimpanzees and humans are not related to brain size alone and may relate to the existence of internal functional interactions, loops, or modules (Oxnard 2004).

Neurological Reorganization in Hominins

In light of the theoretical emphasis neurological reorganization has been given in the literature, surprisingly little precise information is available about its nature during hominin evolution. However, recent work by a few workers provides a glimpse of what might have happened. Contrary to earlier notions about "mosaic evolution," the research of Finlay, Oxnard, and colleagues discussed above suggests that major steps in neurological reorganization (i.e., as opposed to, say, fine-tuning of individual nuclei) rarely, if ever, entailed isolated structures within the brain but, instead, were probably distributed across multiple structures (or modules) within the brain. This hypothesis is concordant with functional imaging studies that indicate higher-order cognitive tasks engage numerous cortical areas that are dispersed across the cortical mantle (Frackowiak et al. 1997). Such distributed reorganization is inconsistent, however, with the suggestion (based on controversial identifications of the lunate sulcus on endocasts from fossil hominins) that early australopithecines with apelike sulcal patterns were reorganized only in their posterior parietal association cortices (Holloway et al. 2004; Falk 2011, 2014).

As detailed elsewhere (Falk 2009, 2011, 2014), ongoing controversy about the lunate sulcus has had a prolonged and, in my opinion, negative impact on the field of paleoneurology since the beginning of the twentieth century. Briefly, the anterior border of the primary visual cortex in monkeys and apes is usually delineated approximately by a crescent-shaped lunate sulcus (reddened in the chimpanzee brain in Fig. 4). Until recently, some human brains were thought to manifest lunate sulci, albeit in a posterior position in keeping with the fact that their representation of primary visual cortex occupies significantly less of the outside surface of the occipital lobe compared to monkeys and apes. Lunate sulci were, thus, thought to have "migrated" posteriorly as the parietotemporo-occipital association regions expanded in front of them. When Raymond Dart described the first australopithecine fossil (Taung), he misidentified a suture reproduced on its endocast as a lunate sulcus and interpreted its posterior position as indicating that Taung's ape-sized brain had been reorganized toward a human-like condition (Dart 1925). More recent workers interpreted Dart's analysis to indicate that early hominin brains reorganized in a "mosaic" fashion, in which occipital reorganization preceded that in other parts of the brain. A recently emerged unpublished manuscript that Dart wrote in 1929 now makes it clear, however, that he believed australopithecine brains reorganized globally rather than in a mosaic fashion (Falk 2009). Furthermore, a recent high-resolution MRI

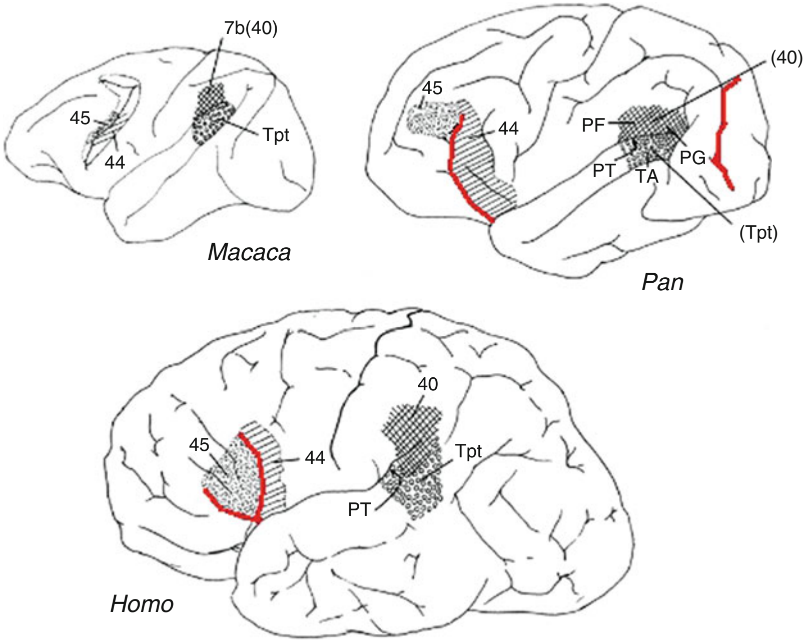

Fig. 4 Gross language areas in humans and their proposed homologs in macaques and common chimpanzees. In the left hemispheres of humans, Brodmann's areas 45 (pars triangularis) and 44 comprise Broca's speech area, while areas Tpt (temporoparietal), PT (planum temporale, buried within depths of Sylvian fissure), and Brodmann's area 40 are parts of Wernicke's receptive language area. Human area 40, macaque area 7b, and chimpanzee area PF/PG are proposed homologs, as are human and macaque areas Tpt and chimpanzee area TA. The proposed homologs are based on cytoarchitectonic and functional similarities and should be viewed as tentative. The fronto-orbital sulcus (bordering area 44) and lunate sulcus (approximately bordering primary visual cortex) are shown in *red* for *Pan*, as are the anterior horizontal and ascending branches of the Sylvian fissure in *Homo*, which approximately border area 45 (data from Preuss (2000), Amunts et al. (1999), Gannon et al. (1998), Aboitiz and Ricardo (1997), Galaburda and Pandya (1982), Crosby et al. (1962), Jackson et al. (1969), Bailey et al. (1950), von Bonin (1949), Falk (2012))

study that assessed the presence/absence of lunate sulci in brains from 110 adult humans (Allen et al. 2006) revealed that this sulcus was lost during human evolution. Elsewhere (Falk 2012, 2014), the loss of the lunate sulcus in humans is interpreted in light of Van Essen's (1997) tension-based theory about how convolutions and sulci develop.

Research of Semendeferi and colleagues (Semendeferi et al. 1997; Semendeferi and Damasio 2000; Semendeferi 2001) sheds light on neurological reorganization in hominins at the level of large sectors including whole lobes. Semendeferi and Damasio (2000) obtained MRI scans of brains from nearly 30 living humans and apes, processed the data to obtain volumes of the various lobes, and performed comparative statistical analyses of the absolute and relative volumes of each lobe. Although the overall relative sizes of the lobes of the brain changed little after the phylogenetic split of hominins from great apes, this study revealed that the temporal lobe (involved in recognition and memory) may have differentially enlarged during hominin evolution, while the human cerebellum is significantly smaller than expected from allometric predictions. The insula, which processes autonomic functions, internal stimuli, taste, and speech articulation (Dronkers 1996), may also be somewhat enlarged in humans. Contrary to Semendeferi's (2001) finding of no increase beyond allometric expectations for the large parieto-occipital sector of the human brain, those of another study (utilizing geometric morphometrics) suggest that modern humans are characterized by relatively great development of the parietal lobes (Bruner 2004), a conclusion that awaits further confirmation.

Equally important, by analyzing 3D MR reconstructions of brains from living apes and humans (Semendeferi et al. 1997) in conjunction with comparative histological sections from postmortem specimens, Semendeferi and her colleagues have helped dispel old myths (indeed, some might even say "received wisdom") about the evolution of human frontal lobes. Until recently, many believed that higher cognitive abilities in humans evolved in conjunction with differentially enlarged frontal lobes. Semendeferi's comparative imaging work dispelled this notion, however, by quantifying the allometric nature of human frontal lobe enlargement (i.e., they are the size one would expect in ape brains enlarged to the size of human brains).

Turning to the important question of neurological reorganization within larger sectors, comparative cytoarchitectonic studies suggest that human frontal lobe evolution entailed internal rewiring and enlargement in some areas (e.g., Brodmann's area 10; Semendeferi et al. 2001, 2002) and a decrease in others (Brodmann's area 13; Semendeferi et al. 1998) rather than an increase in overall frontal lobe size. It was therefore concluded that area 13 of the posterior orbitofrontal cortex, a part of the limbic system that is involved in emotional reactions to social stimuli, is a conserved feature in brain evolution, whereas the relative size of area 10 that forms the frontal pole in ape and human brains, and contributes to planning and the undertaking of initiatives, increased during hominin evolution. A remarkable increase in the proportion of white matter volume of the human precentral cortex was also found (Semendeferi et al. 1997), which again speaks to the fact that human frontal lobes are more complexly wired rather than relatively larger than those of their ape cousins.

Semendeferi and her colleagues compared the spacing of neurons in layer III in frontopolar (BA 10), primary motor (BA 4), primary somatosensory (BA 3), and primary visual (BA 17) cortices in great and lesser apes and humans (Semendeferi et al. 2011). They found that the horizontal spacing distance (HSD) between neurons increased in BA 10 (but not the other areas) in hominins after they split from chimpanzees. Such spacing is interpreted as facilitating complex interconnectivity, which contributes to information processing related to anticipating future events, multitasking, and integrating limbic input to arousal, motivation, and intentions, among other functions. A similar histological finding has been reported for human BA 44/45 (Broca's speech area) (Schenker et al. 2008), which suggests that the frontal lobe may have been widely reorganized during human cognitive evolution.

Other research suggests that the visual system was also reorganized during human evolution (Preuss et al. 1999), which surprised even the investigators because "it is axiomatic among neuroscientists and psychologists that the visual abilities of humans and monkeys are virtually identical" (Preuss 2001, p. 156). Specifically, the authors report histological evidence suggesting that the human primary visual area differs from that of apes and monkeys in the way that information is segregated from layers of the lateral geniculate nucleus. Interestingly, they suggest that humans have enhanced capacities for analyzing moving stimuli and speculate that these changes may have occurred in response to the challenge of visually decoding rapid mouth movements entailed in speech and its accompanying manual gestures (Preuss 2001).

Neurological Reorganization Related to Language, Handedness, and Music

It is tempting to hypothesize that the expansion of the human cortex was accompanied by the addition of new areas and that the classic language areas in the left hemisphere (Broca's speech area [Brodmann's areas 44 and 45] and Wernicke's language receptive area [Brodmann's areas 21, 22 plus, when defined more broadly, 37, 39, 40]) are neomorphic structures (Preuss 2001). However, Preuss notes that "at the present time, there is no good evidence that humans possess species-specific cortical areas" (Preuss 2001, p. 155). Indeed, cytoarchitectonic studies on macaques suggest that the inferior limb of the arcuate sulcus contains homologs of areas 44 and 45 (Galaburda and Pandya 1982; Deacon 1992; Preuss 2000), and homologs of posterior language areas (Wernicke's area) have been identified in the macaque superior temporal and inferior parietal lobes (Galaburda and Pandya 1982; Preuss 2000) (Fig. 4). Simple movements of the mouth and hands activate ventral premotor cortex in monkeys, as they do its likely homolog, Broca's area, in humans (Petersen et al. 1988; Colebatch et al. 1991; Gallese et al. 1996; Rizzolatti et al. 1996), and these "mirror neurons" also discharge when similar actions are observed in others (Rizzolatti et al. 1996). Because of their discovery in human and nonhuman primates, mirror neurons are hypothesized to be part of an action-perception network that facilitates gestural (manual and orofacial) communication in apes and humans as well as linguistic communication in the latter (Falk 2004c, d). From a functional perspective, it is also interesting that, like humans, macaques are thought to be left hemisphere dominant for processing certain socially meaningful (as opposed to neutral) vocalizations (Petersen et al. 1978, 1984; Heffner and Heffner 1984, 1986).

Paleoneurologists have long speculated about whether a chimpanzee-like frontal lobe in early hominins could have given rise to a humanlike Broca's area, but these efforts have been hampered by a lack of consensus about the identities of homologous sulci and gyri in great apes and humans, which were traditionally proposed mainly on the basis of relative positions of sulci rather than on cytoarchitectonic grounds (Connolly 1950). Unlike frontal lobes of humans, a fronto-orbital sulcus (*fo*) of chimpanzees (reddened in Fig. 4) typically incises the lateral border of the dorsal frontal lobe and extends onto its orbital surface where it courses caudally toward the temporal pole (Connolly 1950). The bulge delimited by *fo*, or so-called orbital cap, represents Brodmann's area 44 (Bailey 1948; Bailey et al. 1950; Connolly 1950; Jackson et al. 1969) (Fig. 4) and to varying degrees the addition of part of area 45 (Sherwood et al. 2003) in chimpanzees. Sherwood et al. (2003) explored the relationship of sulci to cytoarchitectural areas 44 and 45 in brains from five adult chimpanzees and found that just as the border between cytoarchitectonic areas 44 and 45 of humans is not always defined by sulci (Amunts et al. 1999), the border between the two areas in chimpanzees does not always coincide with the surface of the fronto-orbital sulcus. Rather, intersubject variability was high and area 45 tended to spill over caudally into the presumed domain of area 44 in both species. It is also important to stress that the similar bulge that appears at the level of the temporal pole in humans, the orbital cap (or so-called Broca's cap), is *not* homologous to that of chimpanzees (Falk 2014) because it contains areas 45 and 47 rather than the areas located in the chimpanzee cap, namely, area 44 (Connolly 1950) and (sometimes) 45 (Sherwood et al. 2003). Although it has recently been suggested that area 44 is larger in the left than the right hemisphere of chimpanzees (Cantalupo and Hopkins 2001), as reported for humans (Amunts et al. 1999), for methodological reasons, the jury is still out on whether or not the homolog of Broca's area in great apes exhibits humanlike asymmetry (Sherwood et al. 2003).

There is more agreement about asymmetry in the chimpanzee homolog of at least part of Wernicke's area. Gannon et al. (1998, 2001) investigated the homolog of the planum temporale (PT) in 18 chimpanzee brains and determined that the left PT was significantly larger in 17 of the 18 brains (94 %). This region is a component of Wernicke's area in the left hemisphere of humans, in whom it manifests a similar anatomical pattern and left hemisphere size predominance. The authors concluded that human language may have been founded on this basal anatomical substrate and that it may have been lateralized to the left hemisphere in the common ancestor of chimpanzees and humans millions of years ago (Gannon et al. 1998).

More than a century after Broca's area was identified, it is recognized that it has certain nonlinguistic functions and that the act of speech activates wider areas of the cerebral cortex. Nevertheless, the importance of this area for speech and Wernicke's area for human language reception cannot be denied, and the evolutionary details of their coordinated neurological reorganization (including with other parts of the brain) remain open to investigation (Sherwood et al. 2003; Holloway et al. 2004).

One may, however, engage in reasoned speculation about the evolution of a suite of unique behaviors in hominins and their underlying interconnected and reorganized neurological structures. We know, for example, that people are more neurologically lateralized than other primates and that certain cortical asymmetries underpin behaviors that are unique to the human primate (Falk 1987a), such as the universally high frequency of right-handedness, symbolic language, and humanlike creative abilities related to music, art, and technology (Falk 2000a, 2004a). One may explore the evolution of brain lateralization by studying shape asymmetries in endocasts of fossil hominins (Holloway et al. 2004), since in living people these petalias (which exist to a lesser extent in nonhuman primates LeMay et al. 1982) are statistically associated with handedness patterns and sex (LeMay 1977; Bear et al. 1986). We also know that men and women differ somewhat in the anatomies of their brains and that these differences are hypothesized to have evolved as correlates of different reproductive strategies (Falk 1997, 2001; Falk et al. 1999). Although a review of the literature on primate brain lateralization is beyond the scope of this chapter, it is worth noting that Hofman's (2001, 2012) exploration of design principles that govern the evolution of large brains led him to conclude that large brains tend to increase the number of distinct cortical areas in order to maintain processing capacity and that this may be related to the high degree of brain lateralization in humans.

It is possible that large-brained species develop some degree of brain lateralization as a direct consequence of size. If there is evolutionary pressure on certain functions that require a high degree of local processing and sequential control, such as linguistic communication in human brains, these will have a strong tendency to develop in one hemisphere (Aboitiz 1996; Hofman 2001, p. 123).

Conclusions

Primate nervous systems became more variable over the course of evolution. During the Eocene, brain sizes were all small. Today, there are still small-brained species, but also larger-brained ones due to a widening range of variation as the Cenozoic progressed. The same can be said for RBS. Over 30 years ago, Radinsky (1974) pointed out that elaboration of visual abilities and reduction of olfaction were among the features involved at the base of prosimian radiations and, again, in the later emergence of higher primates from prosimian stock. The broad visual and limbic systems that subserve these features were (and are) extremely important for primate species-specific communication. Over time, the various neurological components of these systems became variably elaborated and reorganized within different groups. Preuss' (2001) suggestion that the "surprisingly" reorganized human visual system may have evolved in response to the challenge of visually decoding rapid mouth movements entailed in speech and its accompanying manual gestures underscores the ongoing continuity of adaptations that occurred extremely early in primate evolution. Semendeferi's (2001) seminal work on hominoid prefrontal cortices (Brodmann's areas 10 and 13) illustrates that executive parts of the cerebral cortex eventually got into the act and were also subjected to evolutionary reorganization (Semendeferi et al. 2001).

The arguments about the relative evolutionary merits of brain size versus neurological reorganization are unnecessary (Gould 2001). The suggestion by Finlay and colleagues (Finlay and Darlington 1995; Finlay et al. 2001; Kaskan and Finlay 2001) that the sizes of different brain structures are a consequence of overall brain size, not only in primates but also in other mammals, is an important contribution to our understanding of ontogenetic brain development and brain evolution. What has sometimes been lost is that Finlay's model leaves room for evolution of the kinds of neurological specializations that interest paleoneurologists. Oxnard and de Winter's models for parsing brain size evolution may also shed light on the evolution of broad (but presumably intertwined) subsections of the nervous system that subserve very different lifestyles, separate from phylogenetic considerations (de Winter and Oxnard 2001; Oxnard 2004). These findings extend, rather than contradict, those of Finlay and colleagues. Add to the mix, neurological reorganization that can take place with, or without, an increase in brain size and the potential for evolving internal functional interactions, loops, or modules (Oxnard 2004) becomes realized. Primate cortices may, indeed, represent "veritable hotbed(s) of evolutionary reorganization" (Preuss 2001, p. 140). As students of paleoneurology have discerned, however, the high intelligence of today's primates flowered from trends in primate brain evolution that reach back into deep time (Radinsky 1974). Given the complexities involved in disentangling the evolutionary dynamics of increasing brain size from the intricate (and often hidden) subtleties of neurological reorganization, that insight is somehow very satisfying.

Cross-References

- ▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins
- ▶ Primate Intelligence
- ▶ Primate Life Histories
- ▶ Theory of Mind: A Primatological Perspective
- ▶ The Evolution of Speech and Language
- ▶ The Evolution of the Hominid Brain
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology
- ▶ The Paleodemography of Extinct Hominin Populations
- ▶ The Species and Diversity of Australopiths

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Primate Life Histories

Elke Zimmermann and Ute Radespiel

Contents

E. Zimmermann (✉) • U. Radespiel
Institut für Zoologie, Tierärztliche Hochschule Hannover, Hannover, Germany
e-mail: elke.zimmermann@tiho-hannover.de; ute.radespiel@tiho-hannover.de

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Abstract

The life history of any species is determined by traits that characterize its developmental and reproductive rates as well as the reproductive effort spent over its lifetime. This chapter will present an overview of the current knowledge on the diversity of primate life history. It will explore potential links between life history and major biological factors, which are suggested as a partial explanation for the existing interspecific variations in life history. Furthermore, it will outline general principles and current hypotheses on the evolution of primate life history. This review will show that extant primates ranging from nocturnal ancestral primates to apes provide an important biological substrate illuminating the evolutionary roots and selective forces that shaped human life history.

Introduction

The life history of any species is determined by traits that characterize its developmental and reproductive rates, as well as the reproductive effort spent over its lifetime (Stearns 1992). For mammals, these traits are usually expressed in the gestation length, number and size of offspring at birth, body mass and age at weaning, patterns of postnatal growth, age at first reproduction, interbirth interval, and life span. Life history pattern and variation can be studied on an interspecific or intraspecific level.

Intraspecific variations arise because life history traits are modified by ecology, and different populations of a single species can therefore be expected to show some differences in life history according to the specific ecological settings they experience (Lee and Kappeler 2003). Life history traits of a given species should therefore be taken as predispositions toward certain ranges of potential values (Kappeler et al. 2003), and these ranges can, on the other hand, be taken to explore the effects of different socioecological parameters on life histories. Broad interspecific comparisons of life history traits, on the other hand, form the basis for most existing life history models. Both levels of comparisons will be employed in this chapter in order to illuminate the major evolutionary forces shaping primate life history patterns.

Many aspects of biological timing show a systematic covariation with body mass (Calder 1984), such that body mass has been recognized to be a major predictor of life history variation among species. For example, a large species usually takes longer to grow to maturity and will have larger neonates than does a small one (Harvey et al. 1987; Ross 1998). The relationship with body mass is not an isometric function in which life history traits vary in direct proportion to body mass. Instead, a trait (P) will typically vary in an allometric fashion (W) that is based on the formula: $P = aW^b$. The growth constant a (allometric coefficient) and b (allometric exponent) describe the specific nature of the scaling relationship in any given case. If this formula is logarithmically transformed, it describes a straight line with a slope b. The growth constant a varies between 0.19 and 0.61 in primates (Mumby and Vinicius 2008) and the primate mean $a = 0.35$ is clearly smaller than the average value of $a = 1$ for other mammals (Charnov 1993). Due to fundamental interdependencies among body mass and most biological traits, allometric analyses are obligatory when exploring variations in primate life histories and are taken into consideration in all parts of this chapter. In allometric analyses, it is commonly observed that the data are divided into two or more subsets that show a similar scaling trend (allometric exponent or slope value) but that are vertically separated (i.e., show different intercepts). These subsets can be referred to as “grades” and the vertical separation between them can be termed a “grade shift” (Purvis et al. 2003).

This chapter will present an overview of our current knowledge on life history diversity among extant primates (including humans); explore potential links between life history and major biological factors, which are suggested as a partial explanation for the existing interspecific variations; and outline general principles and current hypotheses of life history evolution.

General Features of Primate Life Histories in Comparison to Other Mammals

The “speed” of life, or reproductive turnover, is a central concept in the field of life history research (Stearns 1992). Primate life histories lie at the slow end of the fast-slow continuum that has been described for mammals in general (Harvey and Clutton-Brock 1985; Charnov and Berrigan 1993; Ross 1998; Dobson and Oli 2008; Jones 2011). This is expressed in altered allometric relationships for many primate life history traits in comparison to those of other mammals. In particular, primates have longer gestation periods, smaller litter sizes, larger neonates, slower postnatal growth rates, a later age at first reproduction, a lower annual fertility, and a longer life span than most other mammals of the same body weight (Fig. 1; Martin and MacLarnon 1985, 1988; Charnov 1991; Lee et al. 1991; Charnov and Berrigan 1993; Ross 1998; Jones 2011). As a consequence, primates possess an extended period of infancy and juvenility and have lower reproductive rates in comparison to other mammals of the same size (Charnov 1993; Charnov and Berrigan 1993).

Many hypotheses have been suggested that may explain why primates are so different. They can be broadly categorized into three groups of related arguments.

The first group of explanations deals with the evolutionary relationship among life history variables and brain size. Allometric analyses have shown that large-brained primates generally have long gestation periods, slow, prolonged growth periods, late sexual maturation, and long lives (Harvey et al. 1987; Allman et al. 1993; Charnov and Berrigan 1993; Hakeem et al. 1996; Barton 1999; Ross and Jones 1999; Ross 2003; Barrickman et al. 2008; Schuppli et al. 2012). Existing brain size hypotheses aim to explain the underlying evolutionary pathways (see below).

The second group of explanations is related to different mortality schedules that are environmentally imposed (Promislow and Harvey 1990; Charnov 1991, 1993; Stearns 1992; Janson and van Schaik 1993; Ross and Jones 1999). Primate-specific avenues have been suggested to act in the form of relatively high juvenile mortality (Janson and van Schaik 1993) or a high juvenile recruitment uncertainty (Jones 2011) that may both favor the evolution of slow growth, i.e., extended periods of juvenility, or relatively low rates of adult mortality that may be connected to a late age of first

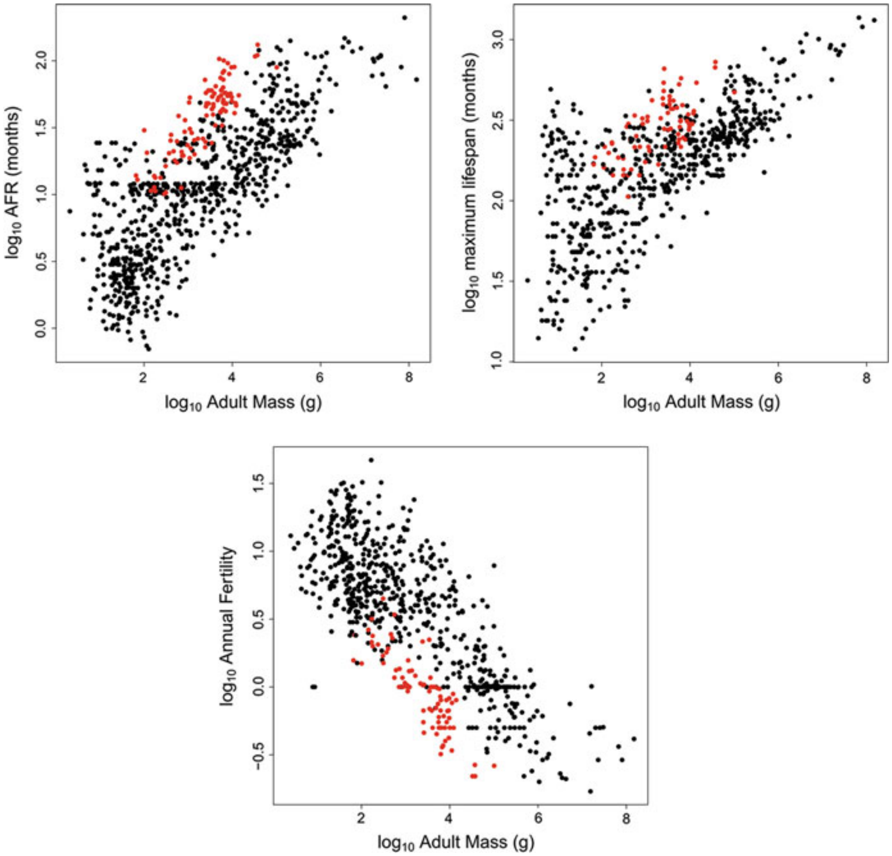

Fig. 1 Scaling relationships between adult female body mass and three life history variables in mammals, age at first reproduction (*left*, *AFR*), maximum life span (*middle*), and annual fertility (*right*) for primates (*red dots*) and other mammals (*black dots*) (Modified after Jones 2011)

reproduction and therefore delayed maturation (Promislow and Harvey 1990; Stearns 1992; Charnov 1993, see below).

The third group of explanatory hypotheses stresses the importance of ecological factors (i.e., diet, predation) on productive rates (birth rates, age at first reproduction) and therefore the speed of life (Rowell and Richards 1979; Eisenberg 1981; Ross 1988, 1992a, b; van Schaik and Deaner 2002, see below). It should be noted that the second and third group of hypotheses may be partly connected via the parameter of mortality.

Variability in Primate Life History Traits

The previous considerations contrasted primate life histories as a whole with those of other mammals. This generalization disregards the finding that primates themselves contain a broad variety of life history pattern (Fig. 2).

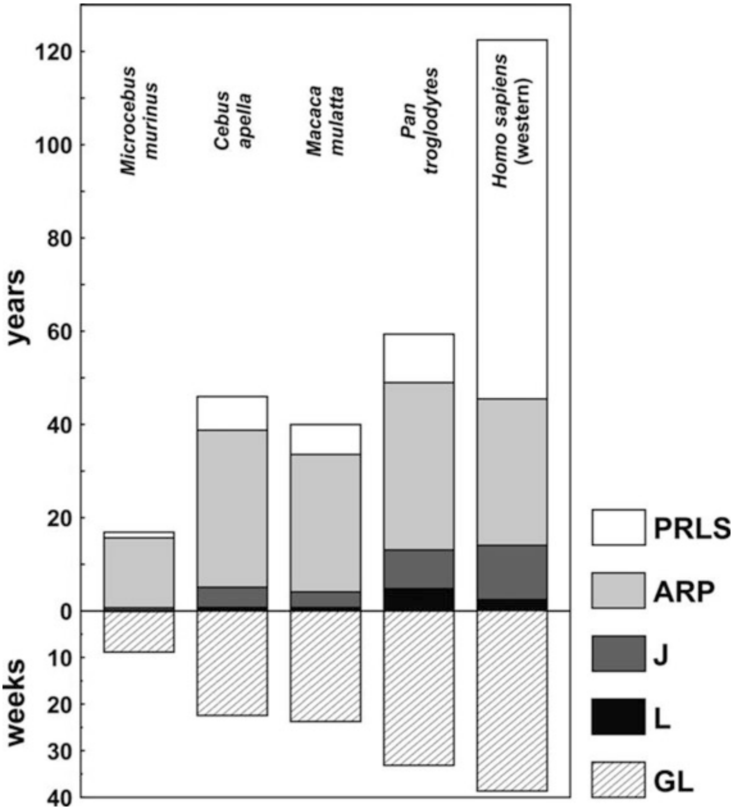

Fig. 2 Diversity of primate life histories (*PRLS* postreproductive life span ((maximum life span from Appendix – *J*)*PrR, *PrR* proportion of adult years which are postreproductive, species-specific PrR-values taken from Levitis and Lackey 2011), *ARP* adult reproductive period (upper limit: maximum life span – PRLS), *J* juvenility (upper limit: average AFR from Appendix), *L* lactation (upper limit: average WA from Appendix), *GL* gestation length (average *GL* from Appendix))

Gestation Length

Gestation length in primates (see Appendix) varies considerably from 52 days in the gray-brown mouse lemur (*Microcebus griseorufus*) to 285 days in the gorilla (*Gorilla gorilla*). Gestation length is correlated with adult female body mass ($r = 0.74$) and even more so with neonatal body mass ($r = 0.82$) (Harvey et al. 1987). Gestation length in the order Primates seems to follow quite well the allometric Equation $G = kW^{0.15}$ (Martin et al. 2005) with W indicating adult body mass. Among all studied primate taxa, only lemurs with larger litters that are parked in a nest for some time after birth (like *Cheirogaleus*, *Microcebus*, *Mirza*, and *Varecia*) have a much shorter gestation period than predicted from the best-fit line (Martin 2007). In general, correlations between the developmental state of the young and life history variables indicate that species with poorly developed (relatively altricial) young characteristically have small body mass and relatively short gestation periods, have limited motor and thermoregulatory abilities at birth, are nocturnal, and use nests (Martin 1990; Ross 2003). Species with more precocial young tend to have the opposite set of characteristics.

Neonatal Body Mass

Neonatal body mass ranges from about 4 g in *Microcebus lehilahytsara* to more than 3,000 g in *Homo sapiens* (see Appendix) and is largely predicted by adult female body mass ($r^2 = 0.917$) and in addition by gestation length ($r^2 = 0.593$), i.e., large mothers and long gestation periods produce large neonates (Wells et al. 2012). It has been shown, however, that strepsirhine primate neonates are generally smaller relative to adult body mass than haplorhine primate neonates (Martin et al. 2005). There is additional variation in relative neonatal body mass that requires an explanation. Besides the obvious altricial-precocial dichotomy, one parameter has repeatedly received attention in this context, namely, litter size. It had been hypothesized that litter size should correlate negatively with neonatal body mass (Leutenegger 1973). Although this has been disputed by some authors (Harvey et al. 1987), others have found statistical support for this relationship, at least at an intraspecific level (Ross and Jones 1999). In general, however, it must be stated that the reduction in litter size and the "decision" for few and large infants were probably made very early in primate evolution, which limits observable variation in the primate order. Other arguments have emphasized that the species-specific mode of placentation may constrain neonatal mass (Leutenegger 1973, 1976). Species with hemochorial placentas (anthropoid primates) may be able to nourish their fetus longer (and therefore to larger size) than species with an epitheliochorial placenta (most lemurs and lorises). Although this may explain some neonatal mass variations in primates, this does not hold for other mammalian orders (Martin 1984), and its general explanatory value is therefore unclear.

Litter Size

Litter size in primate species is generally small and ranges from one to a maximum of four (average: 1–2, see Appendix). A litter size of one is typical for most primates, and a litter size of two is the rule only for several mostly nocturnal strepsirhines and most callitrichids. A phylogenetic reconstruction revealed that the ancestral primate most likely had only a litter size of one and that litter size increased again secondarily several times (Kappeler 1998; see also Leutenegger 1979). Two different avenues have been suggested for the evolution of larger litters within the primate lineage. Larger litters occur together with relatively altricial development when infants still have their eyes closed at birth and do not cling to their mother's fur continuously (parkers in the strepsirhines, see section "Mode of Infant Care"). The alternative route has evolved in the family Callitrichidae, where relatively precocial twin litters are carried and raised not only by their mothers but with high proportions of allocare (Goldizen 1987; Ross 1991, 2003; Rothe et al. 1993; Dunbar 1995; Garber 1997; Bales et al. 2000; but see Mitani and Watts 1997). In view of the high energetic demands of twin production, coupled with a postpartum estrous in callitrichids, Dunbar (1995) and Ross (1991) suggested that the evolution of paternal care in this group preceded the evolution of twinning. An alternative explanation was offered by Chapman et al. (1990) who found a positive relationship between litter size and the proportion of insects in primate diets in a comparative study that included 70 primate species. They argued that insects may provide crucial energy supply in times of seasonal food shortage, which may then allow certain lineages to produce larger litters.

Age and Body Mass at Weaning

Weaning is not a simple event but is instead a process that may occur over an extended period of time. Definitions of weaning may be as different as the "first intake of solid food," the "beginning of maternal control of suckling," the "complete termination of suckling," or the "mother's resumption of sexual activity" (reviewed in Lee 1996). As a general approximation, weaning age in primates ranges from about 33 days in *Microcebus murinus* to about 2,555 days (7 years) in *Pongo abelii* (see Appendix). Body mass at weaning ranges from about 33 g in *Microcebus murinus* and some callitrichids to about 19.8 kg in *Gorilla gorilla*. Body mass at weaning, however, is so far only available for a relatively small proportion ($n = 55$, 13.1 %, see Appendix) of all 420 primate species listed at the IUCN at present. The age of weaning is highly correlated with neonatal body mass ($r = 0.94$) and with adult female body mass ($r = 0.91$), i.e., large mothers produce large neonates that are weaned later than those of smaller mothers (Harvey et al. 1987). Within primates, at least three grades have been identified in the relationship between weaning age and female body mass (Martin 2007): Lemurs have the relatively shortest weaning age, intermediate weaning ages can be found in Old World monkeys, and weaning ages are longest in the hominoids (Martin 2007). Weaning age scales positively with weaning mass, which is highly proportional to neonatal mass (Lee et al. 1991). This relationship appears to be relatively constant, such that when an infant reaches about four times its birth weight, it is weaned irrespective of the duration of lactation (Lee et al. 1991). Another general pattern has been suggested with the mass at weaning equaling about one-third of the adult body mass (Lee et al. 1991; Lee 1996), although this relationship is debated (Godfrey et al. 2003; Purvis et al. 2003). It is apparent from many allometric analyses that primates show considerable variation in the duration of lactation (infants can be weaned at an earlier or later age), but not in the body mass that is achieved at weaning. Lactation itself is a costly process for the mother who has to convert maternal energy to milk. It requires, for example, additional energetic intake at a rate of approximately 1.3 times the normal intake for humans or 1.5 times for baboons (Prentice and Whitehead 1987; Altmann and Samuels 1992).

Mothers should balance these costs over time, and trade-offs should take into account not only the survival probabilities of the current offspring of a given mass and the energetic demands of mother and offspring during lactation but also survival costs for the mother and the relationship between weaning age, subsequent interbirth interval, and therefore future reproductive rates (Lee 1999; Ross and MacLarnon 2000; Walker et al. 2008; Garcia et al. 2009). Factors that have been suggested to shape the species-specific evolutionary pathways in postnatal growth rates and weaning age are brain growth pattern as a metabolic constraint on infant somatic growth (Martin 1996; Lee 1999), environmental variability acting via differential juvenile mortality on maternal investment (age at weaning) and growth rates to weaning (Ross 1988; Leigh 1994; Garber and Leigh 1997; Lee 1999), milk composition and the degree of close mother-infant contact (Hinde and Milligan 2011), and the extent of available allocare (Ross and MacLarnon 2000; Ross 2003).

Pattern of Postnatal Growth

Compared to other mammals, primates have the longest juvenile periods for their body size (Pereira and Fairbanks 1993). They range from 175 days in *Galago moholi* to 12.5 years in *Homo sapiens* (see Appendix). Juvenility spans the time from weaning to sexual maturity, but is not necessarily a period of continuous growth and acquisition of skills. Two major ways have been identified in which growth may vary within and among primate species (Leigh 1994, 1996): Postnatal body mass growth rates may slowly decrease from birth to sexual maturity, as can be seen, for example, in the common marmoset (*Callithrix jacchus*, Fig. 3) or in *Cebus albifrons* (Young et al. 2010). The second pattern consists of slow growth rates early in life followed by sharp accelerations, so-called growth spurts, prior to sexual maturation. This pattern is characteristic for sexually dimorphic primate species such as baboons (Leigh 1996) or vervet monkeys (Whitten and Turner 2009). Combinations of both basic patterns have generated a great variety of different growth-rate curves in primates. However, they do not correlate well either with other life history variables or with body mass, with brain growth rates, or with dental development (Pereira and Leigh 2003). For example, male *Cercopithecus diana* attains relatively small body mass after growing longer than male *Colobus guereza* (Pereira and Leigh 2003). It has been stated that such ontogenetic divergences presumably reflect life history adaptations to contrasting socioecologies (Leigh and Shea 1995; Pereira 1995; Pereira and Leigh 2003). For example, infant parking and nesting has been recently shown to influence postnatal growth rates in Malagasy lemurs: Species that park infants exhibited faster postnatal growth rates than species with infant-carrying habits (Tecot et al. 2012). Life history theory predicts a general trade-off between juvenile growth and the age at first reproduction, since reproduction and growth are both costly processes that should rarely overlap (Charnov 1993, 1997). Mumby and Vinicius (2008) provided evidence for a significant negative correlation between the growth constant *a* and both age at first reproduction and the duration of the juvenile period, indicating that slower growth coincides with a longer juvenile period

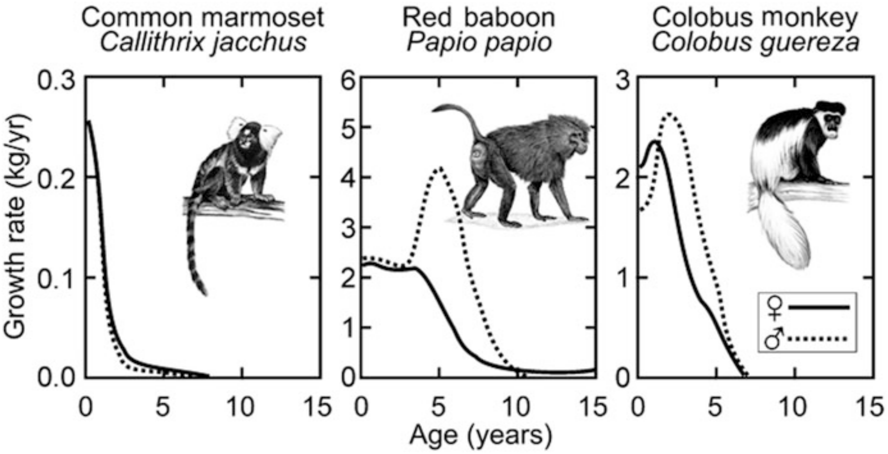

Fig. 3 Development of growth rates and pattern of growth spurts for different primate species. Explanations are given in the text (Modified after Leigh 1994)

and a later onset of reproduction in primates. Other parameters that are discussed as shaping growth curves are risks imposed on juveniles by predation or intraspecific competition for food and social partners, as well as dominance of the mother (Janson and van Schaik 1993; Leigh 1994; Godfrey et al. 2003; Pereira and Leigh 2003; Mumby and Vinicius 2008; Garcia et al. 2009). Finally, intrasexual competition has been shown, for example, to accelerate or extend male growth (bimaturism: Jarman 1983) and can even lead to alternative routes of reproduction (Utami et al. 2002; Wich et al. 2004 for the Sumatran orangutan, *Pongo abelii*).

Age at First Reproduction

The age at first reproduction varies greatly among primates from about 7–8 months for *Galago moholi* or *Microcebus murinus* to more than 15 years for *Pongo abelii* (see Appendix). The age at first reproduction marks a very important step in life since it affects the length of time available for reproduction and therefore limits the reproductive life span of males and females. Furthermore, it has an enormous influence on the intrinsic rate of population increase. In comparison to other mammals, maturity is reached late in primates (Ross 1988; Charnov and Berrigan 1993) and several hypotheses have been developed to explain this extended juvenility. First, allometric influences of adult body size and adult brain size must be addressed. There is a high correlation between adult body mass and age at first reproduction (Pagel and Harvey 1993), although this seems to be largely based on the effect of adult brain size (Harvey et al. 1987; Ross 2003; Barrickman et al. 2008; Barton and Capellini 2011). Large brains have been confirmed independently several times to correlate with late maturation and extended juvenile growth (Harvey et al. 1987; Allman and Hasenstaub 1999; Barton 1999; Ross and Jones

1999; Ross 2003; Barrickman et al. 2008; Barton and Capellini 2011). Barrickman et al. (2008) recently proposed an adaptive explanatory framework and suggested the necessity of such an extended juvenile growth period for the acquisition of foraging or social skills and improved predator avoidance that may explain reduced adult mortality and extended reproductive life span of larger-brained primates (but see Barton and Capellini 2011). Finally, there has been some support for the hypothesis that juvenile mortality rates are correlated negatively with the length of the juvenile period, i.e., primates with high rates of prereproductive mortality reproduce at an early age and thereby speed up reproduction (Ross and Jones 1999).

Interbirth Interval

The interbirth intervals of nonhuman primates range from 3 months in *Microcebus murinus* and *Microcebus lehilahytsara* up to more than 110 months in *Pongo abelii* (see Appendix). The interbirth interval and its variance is strongly influenced by maternal mass (Harvey et al. 1987; Lee 1999), i.e., large mothers have longer interbirth intervals and have a greater potential to extend it further than smaller mothers. The minimum interbirth interval is usually given by the joined duration of gestation and lactation since in many species lactation prevents ovulation (lactation amenorrhea). This phenomenon is adaptive if lactation costs are too high to be combined with the costs of gestation or if lactation is needed for a much longer time span than the gestation would take. In this case, females would risk having two generations of dependent offspring at the same time. Some primate species, such as some callitrichids (Dixson 1992; Tardif et al. 2003) or mouse lemurs (Schmelting et al. 2000), have evolved a postpartum estrus. In these species, infant development is relatively fast and females can afford to lactate and resume reproduction simultaneously due to an early age of weaning.

Three other parameters have been identified that may shape the length of interbirth intervals. First, seasonality in food availability may constrain reproductive rates and even force species into a yearly cycle of reproduction (Lindburg 1987; Di Bitetti and Janson 2000). For example, gray mouse lemurs (*Microcebus murinus*) have been shown to reproduce twice per season given about 1,500-mm rainfall per year (Schmelting et al. 2000), whereas they produce only one litter per year given about 800-mm rainfall per year (Eberle and Kappeler 2004). Second, within social groups of the same species, interbirth intervals also depend on maternal condition. It could be shown, for example, that better-fed (i.e., high-ranking) female olive baboons (*Papio anubis*) have shorter interbirth intervals and higher infant survival than low-ranking females (Packer et al. 1995). Similar results have been found in other species (Cheney et al. 1988 for *Chlorocebus aethiops*; Lee and Bowman 1995 for *Macaca fuscata*). Third, interbirth intervals in lemurs have been shown to correlate negatively with the degree of infant parking and nesting (Tecot et al. 2012). It was hypothesized by the authors that nesting and parking infants reduces the energetic burden of mothers and thereby allows these species to increase infant growth rates and decrease interbirth intervals.

Life Span

Primate life span is notoriously difficult to measure, since either the age of captive animals is often well known but may not necessarily reflect the life span that is typically achieved under natural conditions or its determination in the field requires a long-term commitment of researchers to individually known populations that may span even more than a whole scientific career. Available life span data of nonhuman primates range from an average of 4 years in captive golden angwantibos (*Arctocebus aureus*) to a maximum of about 59 years for chimpanzees (*Pan troglodytes*) and orangutans (see Appendix). In comparison to other mammals, primates have longer lives for their size (Charnov and Berrigan 1993; Jones and MacLarnon 2001). Allometric analyses showed that life span within the primate lineage is positively correlated with body mass and brain size (Harvey et al. 1987; Austad and Fischer 1992; Allman et al. 1993; Allman 1995; Deaner et al. 2003; Barrickman et al. 2008; Kamilar et al. 2010). Brain size seems to be more influential than body size since the partial correlation between life span and brain size remains positive after the effects of body size have been removed but not vice versa (Sacher 1959; Harvey et al. 1987; Allman et al. 1993; Deaner et al. 2003; Barrickman et al. 2008). In addition, age at maturity correlates strongly with life span, and it has even been suggested that life span and brain size may be primarily linked to age at maturity and may be only secondarily correlated with each other via the intervening variable age at maturity (Harvey et al. 1987). Both, life span and age at maturity affect and limit the time period available for reproduction, i.e., the reproductive life span. Reproductive life spans can be quite similar even among species with a divergent pattern of postnatal growth and maturation if, for example, longer lives may compensate for late maturation or vice versa.

The general question is, why did longevity evolve in primates and how can interspecific differences in primate life span be explained? In other words, what are the selective benefits of a long old age? In evolutionary terms, benefits are usually expressed as fitness consequences. On an individual level, an extended life span may result in a larger number of offspring and may therefore provide direct fitness benefits (Fedigan and Pavelka 2001 for *Macaca fuscata*). On the species level, however, a longer life span does not necessarily relate to a higher number of surviving offspring. A female chimpanzee may live up to 50 years but may have only about seven offspring due to late maturation and long interbirth intervals, whereas a rhesus macaque with a life span of 21 years or a mouse lemur of 10 years may each have given birth to about 18 offspring over their lifetime. If the number of offspring does not explain long life span, selective benefits are more likely to be found in offspring quality, which may be linked to other life history variables, in particular to an extended period of juvenility, delayed maturation, reduced rates of adult mortality, and larger brains. It has, for example, been shown that encephalization is significantly correlated with an extension of the reproductive life span, suggesting a balance between brain size, the costs of growing a brain, and the survival benefits provided by enlarged brains (Barrickman et al. 2008; but see Barton and Capellini 2011).

Extrinsic mortality rates have repeatedly been investigated as a potential explanation for life history variations (Kamilar et al. 2010; see section Age-Specific

Mortality Rates). Their connection to life span is suggestive since extrinsic mortality influences the probability of survival to old age and thereby determines the selection pressure upon genes that regulate somatic repair (Kirkwood and Rose 1991). This relation between mortality rates and longevity is supported by several theoretical and empirical studies (Promislow and Harvey 1990; Charnov 1991, 1993; Stearns 1992; Ricklefs 1998; Harvey and Purvis 1999; Ross and Jones 1999; Alvarez 2000; Blomquist et al. 2003). An integrating explanation is offered by the "Cognitive Buffer Hypothesis" (see section "Brain Size").

Variables Linked to Primate Life History Traits

The evolution of primate life history is shaped by differences in brain sizes, phylogeny, and the different ecological and social factors outlined in the following sections.

Brain Size

Brain size and brain growth pattern are strongly interrelated with almost all life history traits. Large-brained primates usually have long gestation periods, have high neonatal body mass, and give birth to few offspring that have a late age of first reproduction and long lives (Harvey et al. 1987; Austad and Fischer 1992; Allman et al. 1993; Charnov and Berrigan 1993; Purvis and Harvey 1995; Allman and Hasenstaub 1999). These relationships exist independently of body size (Sacher 1959; Allman et al. 1993; Martin 1996; Barton 1999; Dunbar and Shultz 2007; Barrickman et al. 2008; Lefebvre 2012) and have been functionally linked either to high energetic costs of large brains (Foley and Lee 1992; Martin 1996; Ross and Jones 1999) or to long developmental processes (learning) during the juvenile period that require large brains (Harvey et al. 1987; Joffe 1997; Barton 1999; Dunbar 2003; van Schaik et al. 2012).

Five influential hypotheses, not mutually exclusive, have been put forth that link brain size to primate life histories

The "Delayed Benefits Hypothesis" aims to explain the relationship between large brain size and longevity (Deaner et al. 2003). Large brains incur high costs (time and risks) but allow an animal to develop skills or knowledge that may lead to fitness benefits later in life. These benefits must exceed the costs of developing them, and long-lived animals have a longer time span to accumulate the benefits (Dukas 1998; Kaplan et al. 2000). Therefore, an evolutionary increase in longevity should increase the likelihood of an evolutionary increase in brain size. A strong correlation (without the outliers, bats) between brain size and life span across the eutherian mammalian orders supports the major prediction derived from this hypothesis (Deaner et al. 2003).

The "Cognitive Buffer Hypothesis" (Sol 2009) argues that large brains offer behavioral flexibility and higher learning capacities to unusual, novel, or complex socioecological challenges. This buffer effect should enhance survival rates and favor longer reproductive life, compensating for the loss of delayed reproduction.

This hypothesis finds some support in the correlation between brain size and life span described by several authors (Harvey et al. 1987; Austad and Fischer 1992; Allman et al. 1993), in the higher cognitive flexibility of large-brained animals (Sol 2009) and in a positive correlation of neocortex size (representing most structures involved in higher-order cognition) with life span (Deaner et al. 2003). Following this hypothesis, the main selective pressure was on brain size, and life history traits were either constrained by (e.g., extended juvenility or age at first reproduction) or coevolved together with brain size.

The "Maternal Energy Hypothesis" (Martin et al. 2005; Martin 2007; Martin and Isler 2010) focuses on energy supplied by the mother during infant brain development up to weaning. It postulates that the evolution of large-brained offspring has required a longer gestation and lactation period or a higher energy input through higher metabolic turnover from mother to offspring. Empirical findings from extant and fossil primates, cetaceans, and carnivores support this hypothesis (Martin and Isler 2010).

The "Brain Malnutrition Risk Hypothesis" or "Developmental Cost Hypothesis" concentrates on the high energetic costs of growing large brains (Martin 1981, 1996; Armstrong 1983; Leonard and Robertson 1992; Aiello and Wheeler 1995; Ross and Jones 1999; Kaplan et al. 2000; Barton and Capellini 2011) and is based on the assumptions (a) that the brain is more sensitive to energy shortage than the rest of the body and energy restrictions during brain development may lead to long-lasting or even permanent brain damage, which has to be prevented, and (b) that body growth trajectories lag behind brain growth trajectories in a general fashion that reflects a functional balance between behavioral capabilities and body size (Deaner et al. 2003). This model can explain the relationship between large brain size and late maturation, as the extension of the body growth period may allow the evolutionary increase in brain size. Furthermore, its predictions correspond well with the observed growth trajectories during lactation and after weaning including growth spurts that occur in certain species (Count 1947; Cheek 1975; Janson and van Schaik 1993; Leigh 1996; Bogin 1999; Deaner et al. 2003; Pereira and Leigh 2003) or the relation between the rate of fetal brain growth and energy turnover of the mother (Barton and Capellini 2011). Supportive evidence for an extension of the "Brain Malnutrition Risk Hypothesis" was presented by Leigh (2004) who identified two different maternal strategies within the primate lineage with regard to pre- and postnatal brain size development, metabolic needs, and age at maturation: the first strategy is followed by females who mature late with large body size and produce infants with relatively large brains (see also Harvey and Clutton-Brock 1985). Late maternal maturation was hypothesized to allow mothers to carry the metabolic costs of very early (fetal or infantile) brain growth through larger size. As a consequence, offspring may be more precocious in terms of cognition, locomotion, foraging, and social behavior. Squirrel monkeys or Old World monkeys as a group appear to follow this strategy (Leigh 2004). The second strategy consists of early maturation, coupled with a slow postnatal brain growth pattern over a long period of time, which may free the mother from extensive postnatal investment by "distributing" the costs of offspring brain growth to the offspring itself or to other group members. Tamarin females seem to follow this second strategy and give birth to offspring early, with short interbirth intervals (Leigh 2004). The differences between these two strategies would reflect different metabolic risks and trade-offs faced by various species at different stages of their life cycles.

Compatible with the latter hypothesis is the “Expansive Brain Hypothesis” (Isler and van Schaik 2009; van Schaik et al. 2012) explaining variation in relative brain size among homoiothermic vertebrates. It claims that costs of a relatively large brain must be met by a combination of increased energy turnover or reduced energy allocation to another expensive function such as digestion, locomotion, or production (growth rate, reproduction). This hypothesis gained support by a large mammalian dataset, including primates, showing that an increase in brain size leads to a longer period of immaturity among monotokous, precocial species, but not among the polytokous altricial ones, which instead decrease litter size (Isler and van Schaik 2009). Relatively large-brained mammals showed reduced annual fertility rates compared to smaller-brained relatives (Isler and van Schaik 2009) and often a compensatory increase in life span (Isler and van Schaik 2009; Gonzales-Lagos et al. 2010).

The five hypotheses differ not only in the life history trait which is most closely linked to brain size (age at first reproduction versus longevity) but also in their causal connection. For example, the “Brain Malnutrition Risk Hypothesis” and the “Expansive Brain Hypothesis” argue that delayed maturation preceded the evolution of larger brains. The “Cognitive Buffer Hypothesis” postulates that larger brains facilitated the evolution of longevity, whereas in the “Delayed Benefits Hypothesis,” longevity preceded the evolution of large brains. Future studies have to derive competing and testable predictions from these hypotheses to clarify the pathways that were most relevant in primate evolution.

Phylogeny

Phylogeny has long been recognized to constrain the evolution of life history. Thus, closely related taxa, such as congeneric species, may show similar life history traits because they are likely to differ less in body size and ecology than more distantly related species (Harvey and Pagel 1991; but see Kappeler 1996). Primate life histories are highly conservative within lineages and show two major clades where strepsirhines as a group lie more to the fast end of the fast-slow continuum than haplorhines (Martin and MacLarnon 1990; Martin 2003; Purvis et al. 2003). Species within each clade share similar life history traits. Neonatal body mass of strepsirhines, for example, is almost three times below that of haplorhines of the same body size (Leutenegger 1973; Harvey et al. 1987; Martin 2003), but strepsirhines tend to have more infants per litter (Chapman et al. 1990). Strepsirhine mothers allocate less energy to prenatal growth per unit time than haplorhines (Martin and MacLarnon 1988; Ross 1988; Young et al. 1990), whereas the two major haplorhine groups, the New World and the Old World monkeys, do not differ in this respect from each other (Ross 1991). After birth, the situation is reversed for the two clades, i.e., strepsirhines grow faster than haplorhines (Martin 2003; Fig. 4). Differences in reproductive output of females between the two clades have led to

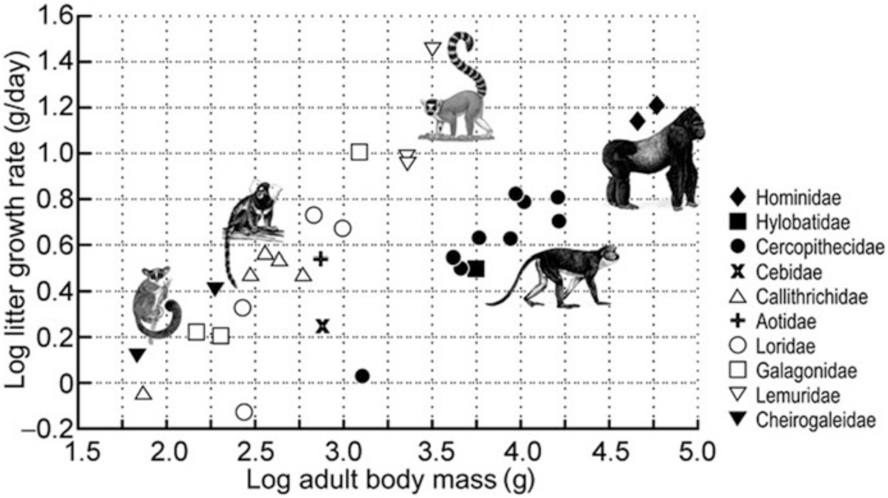

Fig. 4 Grades of primate litter growth rates (Modified after Ross 1998)

the suggestion that haplorhines trade time for energetic investment in infant growth while strepsirhines opt for numbers (Lee and Kappeler 2003). Furthermore, relative brain size in strepsirhines is lower than in haplorhines (Martin 1990; Barton 1999; Deaner et al. 2003). Recently, evidence was provided (Purvis et al. 2003) for a mosaic evolution of life history patterns across five major primate clades (strepsirhines, platyrrhines, cercopithecines, colobines, and hominoids). The rate of accumulation of life history variation differed among the clades in a pattern that seems to correlate with their ecological diversification, i.e., strepsirhines showed the highest rate. Different phylogenetic groups have different patterns of variations, suggesting that they are moving differently on the fast-slow continuum, i.e., some by changing litter sizes, others by varying the age of sexual maturity, and so on. No evidence was found, however, for the claim that life history shaped primate phylogeny by affecting speciation or extinction rates.

Various methods have been introduced to remove the so-called confounding effect of phylogeny in comparative studies (Harvey and Pagel 1991; Purvis et al. 2003) so that potential covariation among life history traits and their evolutionary interplay with demographic, ecological, and social factors may be assessed.

Age-Specific Mortality Rates

Extrinsic mortality rates during different phases of the life cycle have been used repeatedly to explain life history variations. Findings of Promislow and Harvey (1990) suggested, for example, that in mammals both high juvenile mortality and high adult mortality are linked to an early age at first reproduction when the effects of body size are removed. Charnov (1993) developed a comprehensive and very influential model that explains life history variation and in particular age at first reproduction as a consequence of adult mortality rates, which are in turn determined by the environment. When adult mortality is high, animals should mature early in order to minimize the risk of dying before reproducing. The Charnov model is based on a growth law that constrains the relationship between age and body mass before maturity and is able to explain the allometric relationships of many life history traits with body mass, but recent studies shed doubts on its general explanatory value for life history variations in primates (see Purvis et al. 2003 for discussion). Despite this criticism, the general influence of mortality rates on life history pattern and on life span and age at first reproduction in particular is undisputed and supported by many studies (Janson and van Schaik 1993; Owens and Bennett 1995; Purvis and Harvey 1995; Charnov 1997; Kozlowski and Weiner 1997; Ricklefs 1998; Harvey and Purvis 1999; Ross and Jones 1999; Alvarez 2000) even if the exact mathematical model for their relationship is not yet formulated. It can be expected that this relationship is a result of balancing the benefits of reproducing early with relatively high birth rates with the benefits of delayed maturity that leads to larger mothers that may be more successful in raising young and the costs and survival risks that are connected with each of these strategies (Ross 1998; Alvarez 2000). Recently, a comparative individual-based dataset from longitudinal studies of wild populations of seven nonhuman primate species computed actuarial estimates of age-specific survival, and revealed similar mortality patterns across primates, putatively shaped by local selective forces rather than phylogenetic history (Bronikowski et al. 2011).

Diet

Primates feed on a variety of different food items. According to their specialization on fruits, leaves, and animal protein (e.g., insects, arachnids, small vertebrates, eggs), they are usually classified as frugivores, folivores, and faunivores (Fleagle 1999). Since variation in reproductive capacity of a species is strongly affected by the availability and quality of food (Ganzhorn et al. 2003), diet has been hypothesized to influence life history variation between species in a predictable way. To date, however, results on the effect of diet adaptations on life history traits are inconclusive.

Diet appears to have little effect either on prenatal maternal investment (litter weight/gestation length) or on the intrinsic rate of natural increase of a population of anthropoids (Ross 1988). However, a clear association between body mass, ontogeny, and diet was found in another study (Leigh 1994). In the latter, infant growth rate was faster in folivores than in comparably sized nonfolivores. In a study with a much larger sample size including strepsirhines and focusing on intra- and interspecific variations, no significant effect of diet on life history traits was revealed once body mass was removed (Lee and Kappeler 2003). It was shown, furthermore, that the duration of postnatal growth as reflected in the age of weaning was longer for frugivores among anthropoids, whereas it was longer for folivores among strepsirhines.

Dietary strategies were found to affect mortality patterns in seasonal environments in particular during the wet season (Gogarten et al. 2012). Then, folivores showed a higher mortality than frugivores. Comparing life history traits in Asian folivores and frugivores, often living in sympatry, it was found that both groups showed a similar age at birth and interbirth interval, but differed with regard to gestation length (Borries et al. 2011). The latter was longer in folivores than frugivores suggesting a slower fetal growth rate (lower maternal energy) and/or advanced dental or gut development.

Predation

Predation is a major ecological factor influencing mortality patterns in primate populations. It is known to be dependent on body size, such that larger-bodied animals face a lower predation risk than smaller-bodied ones (Read and Harvey 1989; Isbell 1994; Janson 2003; Scheumann et al. 2007). It is therefore expected that predation varies according to body size and affects reproductive output in primate females.

In order to explore the effect of predation on life history, researchers have often used subjective assessments of predation risks (Janson 2003; Lee and Kappeler 2003). For example, predation risk was estimated based on the response to predators and on predator encounter rates, and then ranked as low, medium, and high (Lee and Kappeler 2003). However, only a clade difference on relative reproductive output has been found so far (Lee and Kappeler 2003). Thus, short gestation periods were associated with high risks of predation in strepsirhines. Neonatal body mass and mass at weaning varied as a function of predation risk in anthropoids, such that under high-risk infants were born large but weaned small, minimizing not only the risks after birth but also maternal investment during the postnatal growth phase associated with high risks (Lee 1999). Recently, a new theoretical model was introduced linking life history variation between species with predation risk and social grouping pattern (Janson 2003). It was observed that primate species with large body size or living in large cohesive bisexual groups, both assumed to be adaptations to high predation risk, tend to have low predation rates. Based on the new model, it could be shown that interspecies variations in longevity can explain these observations, assuming that predation risk remains fairly constant across primates. If longevity increases with increasing body mass, as has been shown empirically, then larger species face the cost of predation over a longer time span than smaller ones and consequently will gain a larger fitness benefit by evolving sophisticated antipredator responses (e.g., increased sociality, alarm calls).

Social Grouping Pattern

Three major patterns of social organization are found in primates (Kappeler and van Schaik 2002). Neighborhood systems (Richard 1985; Radespiel 2000), in which individuals forage separately and either sleep alone or come together at the end of their activity period to form permanent and long-lasting unisex or mixed-sexed sleeping groups, are found within the nocturnal strepsirhines, in tarsiers, as well as in one diurnal anthropoid, the orangutan. In these systems, home ranges may overlap within and between sexes. Dispersed and cohesive pairs (Müller and Thalmann 2000; Rasoloharijaona et al. 2003; Ramanankirahina et al. 2011), where both sexes forage either alone or in synchronized association and mostly sleep together, are found in various strepsirhines, in tarsiids, and in various New World monkeys, as well as in gibbons. Sexes share the same home range and defend it against conspecifics. Paternal care of both sexes is a widespread phenomenon within pair-living primates (see section "Mode of Infant Care"). Group-living in cohesive bisexual groups with high variations in size, sex ratio, and temporal stability is the most common pattern of social organization in diurnal primates (Kappeler and van Schaik 2002). Variations in group size depend on the dispersal regime of a particular sex and species as well as on the benefits of foraging and sleeping together and the costs of feeding competition, predation, and infanticide in the respective environment.

Relative group size and residence strategy (both sexes disperse, male philopatry, female philopatry) is associated with relative reproductive output. In a recent study in which the effect of group size [categorized as small (<4), medium (4–20), and large (>20)] and residency on intra- and interspecific life history variations was examined (Lee and Kappeler 2003), large groups of group-living anthropoids had a smaller relative neonatal mass and a higher relative mass at weaning than the other groups. These differences in life history variation between groups of different sizes might be explained either by a differential mortality risk in infants or juveniles due to predation or infanticide (Janson and Goldsmith 1995; Hill and Lee 1998; Janson and van Schaik 2000) or by a different degree of within- and between-group-feeding competitions (van Schaik and van Hooff 1983; Isbell 1991). Furthermore, in group-living primates with male philopatry, a longer relative gestation period, a later age at first reproduction, and a longer birth interval were revealed (Lee and Kappeler 2003). It was speculated that lower rates of extrinsic mortality, suggested to be related to group-living, may facilitate a higher maternal investment.

Life history theory also predicts a relation between social grouping patterns and species longevity over evolutionary times through reduced risk of extrinsic mortality in larger social groups. According to a recent study using a dataset of 253 mammal species (including primates), social group size was, however, a poor predictor of maximum longevity across mammals, as well as within primates, challenging the link between group size and this life history trait (Kamilar et al. 2010).

Mode of Infant Care

Parental investment theory suggests that parental care should be allocated among offspring in ways that maximize the parent's expected lifetime reproductive success (Clutton-Brock 1991). Since the energy that can be devoted to reproduction by an individual is limited, trade-offs between energy investments in infant growth reflected by different modes of infant care and birth rates were suggested to explain some variation in life histories. Primates show a diversity of infant care patterns, which are found to be linked to the reproductive output of mothers.

All nocturnal strepsirhines (except woolly lemurs) as well as tarsiers leave their infants for extended periods of time cached at safe shelters, e.g., tree holes, nests, or dense vegetation, during foraging (Kappeler 1998; Rasoloharijaona et al. 2000; Lutermann 2001; Ross 2003). When changing shelters, mothers carry their infants either orally or clinging to their belly or by both modes of transportation. Species displaying this mode of infant care are called parkers (Ross 2001). In contrast, two nocturnal genera of strepsirhines (*Loris*, *Avahi*), almost all cathemeral lemurs (except *Hapalemur*), all diurnal lemurs, as well as all anthropoids (except *Procolobus verus*) maintain close body contact with their infants during foraging while transporting them clinging to their body (Nicolson 1987; Whitten 1987; Ross 2003). Species with this mode of infant care, with no observed nesting and parking, are called riders (Ross 2001). Anthropoid riders show various degrees of allocare where other females, juveniles, or adult males (often related to the infant) help in infant care.

Parkers with oral infant transport tend to have multiple offspring per litter with low litter mass, born after a short gestation time (Kappeler 1998; Ross 2001; Wrogemann et al. 2001; Ross 2003; but see Randrianambinina et al. 2007, for *Lepilemur*). In contrast, parkers who transport infants clinging to their belly have relative long gestation periods and a single offspring with relatively low body mass (Zimmermann 1989; Ross 2003), suggesting that nesting may be more closely associated to the birth of multiple offspring than to the small size of offspring (Ross 2003). Whether a short gestation period selects for using nests or tree holes to rear offspring or vice versa is not yet clear.

Riding evolved repeatedly in different lineages of primates (Kappeler 1998; Ross 2003) and was most likely selected for reducing mortality risks in infants. Once evolved, it has been conserved, perhaps due to physiological coadaptations. For example, riders have developed a less-energy-rich milk compared to parkers (Tilden and Oftedal 1997). Riders are usually larger than related parkers suggesting that the evolution of large body size and infant fur-clinging may be linked (Kappeler 1998; Ross 2001). Riders have the same birth rates as parkers but wean and breed later when adjusted to body size and phylogeny. They also maintain smaller home ranges than parkers of the same mass (Ross 2001), indicating that carrying infants during foraging incurs energetic and reproductive costs.

Allocare is described in a variety of anthropoid riders (Nicolson 1987; Whitten 1987; Ross 2003) and discussed to enhance the reproductive potential of mothers (Mitani and Watts 1997; Ross and MacLarnon 2000; Ross et al. 2010). Species with high amounts of allocare show more rapid postnatal growth and wean their infants at a younger age (but at the same relative size) than those with low allocare (of the same body mass, Fig. 5). This early weaning allows higher birth rates but does not lead to earlier maturation of the infants because of brain size constraints (Ross 2003). A recent comparative study on allocare and life history evolution across mammals (including not only

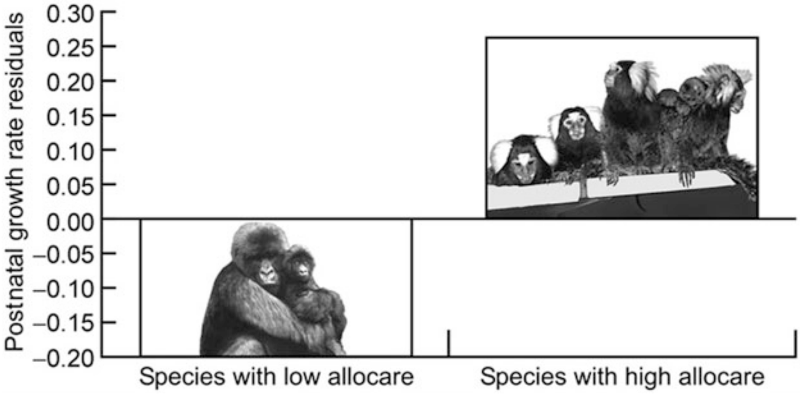

Fig. 5 Relationship between allocare and relative growth rates (Modified after Ross 1998)

haplorhines but also strepsirhines) revealed that only in primates does a strong link exist between the presence of allocare and fertility (Isler and van Schaik 2012). This relationship was due to the exceptional cooperative breeding pattern of callitrichids, in which infants are provisioned by the father and other caregivers, a behavior that benefits the mother by reducing energetic costs of infant rearing. Another recent study, exploring the effect of infant parking, nesting, and allomaternal care and life history in a previously neglected group of strepsirhines, the Malagasy lemurs, yielded unexpected results (Tecot et al. 2012). It showed that, in contrast to haplorhines, allocare in lemurs did not impact reproductive output (assessed by fetal or postnatal growth rates, interbirth intervals). However, infant parking and nesting were positively related to faster fetal and postnatal growth, while nesting was negatively associated with interbirth interval (Tecot et al. 2012). These findings coincide with those on nonprimate mammals and were interpreted as representing an adaptation to infant survival in Madagascar’s harsh and unpredictable environment.

Human Life History

Humans (*Homo sapiens*) differ fundamentally from all other primates in four life history traits: neonatal weight, age at first reproduction, interbirth interval, and life span (Smith and Tompkins 1995; Kaplan 2002; Hawkes et al. 2003). Compared to apes, human babies are relatively large at birth, but they grow more slowly and have a fairly extended childhood (period following infancy when youngster is weaned but still depends on caregivers for feeding and protection (Bogin 1999)). Furthermore, humans reach reproductive age much later and have shorter interbirth intervals and a higher longevity than apes (Leigh and Park 1998; Kaplan et al. 2000; Mace 2000; Lee 2012).

Maximum life span in humans is reported to range between 90 and 122 years (Weiss 1981), which is about twice as long as in chimpanzees and gorillas (Kaplan and Robson 2002). A large proportion of this time is postreproductive in women, i.e., after woman have entered menopause, implying that total life span and fertile life span are disconnected in humans. For example, an 85-year-old woman has spent about 41 % of her life in a postreproductive state, which is very much in contrast to nonhuman primates, whose postreproductive periods are usually short and coincide with frailty and somatic deterioration (Hawkes et al. 1998; Johnson and Kapsalis 1998; Pavelka and Fedigan 1999). Whereas the fertile life span of humans is quite similar to that of great apes (Alvarez 2000; Kachel and Premo 2012), woman can have a much higher fecundity due to much shorter interbirth intervals (Hawkes et al. 2003).

In addition to these specialized life history patterns, human brain size is three- to fourfold larger than in chimpanzees and gorillas (Kaplan and Robson 2002) and much higher than expected for primates when adjusted to body size (Pagel and Harvey 1989). The human brain grows faster and continues to grow longer after birth (Bogin 1999; Kaplan 2002; Reiches et al. 2009; Leigh 2012).

Furthermore, humans show broad intraspecies variations in growth rate, age of maturation, birth rate, age-specific mortality, and senescence, which not only depends on ecological factors but also on food technology, medical care, and culture (Mace 2000; Kaplan 2002; Hawkes et al. 2003; Schuppli et al. 2012). In developed countries during the last 150 years, the average age at menarche among girls has decreased by about 4 years; birth rate in women has changed from six to about two children per family, and the percentage of people reaching more than 100 years of age has increased manifold (Kaplan 2002).

To date, there has been much lively debate, but no consensus, on how to explain these human peculiarities in life history patterns. Some researchers argue, for example, that the strongly extended life span of humans, with the emergence of a long menopause in women, is nonadaptive and represents an artifact of a quite recent increase in longevity caused by improved living conditions (Broadfield 2010). This view is supported by empirical data showing that captive and domesticated animals also live longer than their wild counterparts (Austad 1994). Others argue that an increased longevity in humans evolved as a by-product of selection acting elsewhere in human life history ("reserve capacity hypothesis," Larke and Crews 2006; Bogin 2009; and "embodied capital hypothesis," Kaplan 2002; Kaplan et al. 2003) or propose that our long life span is adaptive in itself ("grandmother hypothesis," Hawkes et al. 1998, 2003).

The "embodied capital hypothesis" (Kaplan et al. 2000, 2003; Kaplan and Robson 2002) proposes that the prolonged longevity and the large brain size of humans are products of coevolutionary selection favored by the exploration of a new, cognitively challenging feeding niche. Ecological factors increasing the

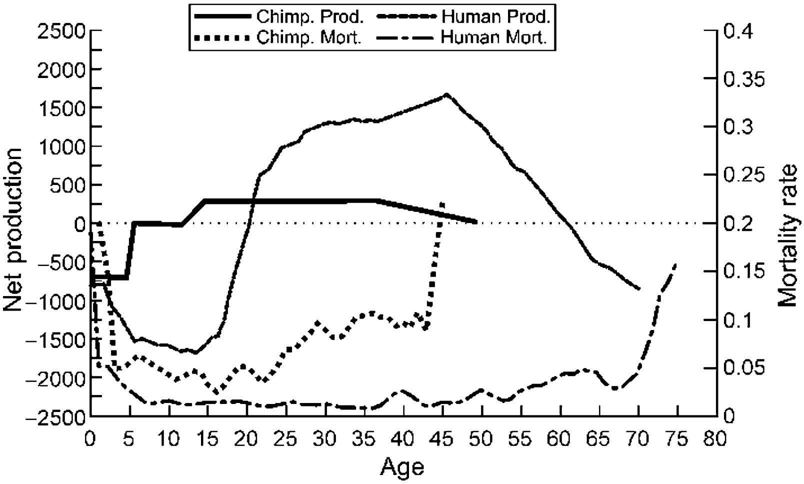

Fig. 6 Net food production and mortality in human hunter-gatherer populations and chimpanzee populations (Modified after Kaplan and Robson 2002)

productivity of investments in developmental embodied capital, such as the brain, should increase both time spent as a child and investments to reduce mortality.

Supporting evidence for this hypothesis was gained by studies on foraging activity, net food production, and mortality in chimpanzee and contemporary hunter-gatherer populations (Kaplan et al. 2000; Kaplan and Robson 2002). Hunter-gatherers showed a much lower mortality rate during childhood and adulthood than chimpanzees along with a quite different net food production profile (difference between food produced and food consumed; see Fig. 6). Chimpanzee and human infants depended nutritionally on their mothers until weaning displaying a negative net food production. In contrast to chimpanzees, humans showed an extended juvenility with further nutritional provisioning by parents up to puberty lowering juvenile mortality. This extraordinary long juvenile dependency paid off later in life when the highly efficient foraging strategies of adults allowed them to obtain a much greater quantity of valuable food than required for personal subsistence, which is reflected in a positive net food production. Whereas these results suggest why longevity may have been extended and brain size enlarged in humans compared to apes, the discovery of the apolipoprotein E Allele-system, which affects neurite growth and aging, offers a potential candidate for the genetic basis of such a coevolutionary process (Kaplan and Robson 2002; Finch and Stanford 2004).

Recently, a comparative study on foraging skill competence in 57 mammal and bird species (Schuppli et al. 2012) within a life history context provided broad biological and empirical support for the “embodied capital hypothesis.” The study revealed that most mammals reach adult-level foraging skills well before the end of their developmental periods, suggesting that energy constraints affect the age at first reproduction. In more complex ecological niches, the age of adult-level skills comes closer to the age of first reproduction. Gregariousness, slow conservative development, and postweaning provisioning favor the late age at skill competence. According to some authors the unusually late age at skill competence among humans arose because our hominin ancestors added cooperative breeding and hunting to the slow development inherited from great apes with complex ecological niches.

The “grandmother hypothesis” (Hawkes et al. 1998, 2003; Alvarez 2002; Lahdenperä et al. 2004; Kim et al. 2012) is based on Charnov (1993) and assumes that prolonged postreproductive life span will evolve when postreproductive females gain greater fitness by increasing the success of their offspring than by continuing to breed themselves. The greater longevity favored delayed maturity because lower adult mortality rates reduce the fitness costs of prolonged growth.

Empirical support for this hypothesis comes from some contemporary and historical populations (Blurton Jones et al. 1989; Mace 2000; Jamison et al. 2002; Voland and Beise 2002; Hawkes 2003), but not all (Hill and Hurtado 1991, 1996, 1999). These studies showed that grandparents may assist philopatric offspring by transferring knowledge and by participating in household tasks and child care. This help may increase offspring breeding probability and grandchild nutrition and survival. A recent comprehensive study on fitness benefits of prolonged postreproductive life span in women using multigenerational individual-based datasets from historical farming communities in Finland ($n \sim 500$ women) and Canada ($n \sim 2{,}300$ women) during the eighteenth and nineteenth centuries (Lahdenperä et al. 2004) provides additional support. Postreproductive women, living in the same household or close to their offspring, have more grandchildren, and greater fitness, because they enhance the lifetime reproductive success of their offspring by allowing them to breed earlier, more frequently and more successfully. Fitness benefits, however, disappear as the reproductive output of the offspring declines. Rates of female mortality accelerate as their offspring cease reproduction. Recently, evolutionary modeling supported that increased longevity in humans can evolve from grandmothering (Kim et al. 2012).

Conclusion

As shown in this chapter, primate life histories are among the slowest in mammals and nevertheless show a fascinating diversity in pattern and variations within and between the more than 420 extant species. The basic traits of life history, such as gestation length, neonatal body mass, number of offspring, age and body mass at weaning, postnatal growth, age at first reproduction, interbirth interval, as well as life span, are linked in complex ways, and to varying degrees, across taxa by physiology (e.g., trade-offs in growth and reproduction) and genetics (e.g., pleiotropy). However, despite more than 40 years of intensive research, the causes of the unique slowness of primate life histories remain poorly understood. The three suggested major determinants, energetic costs of brain growth, age-specific mortality, and socioecology, explain in part the low developmental and reproductive rates of primates but do not yet deliver a comprehensive and conclusive explanation. For example, we do not know whether the energetic costs for brain growth or body growth drive life history evolution, or vice versa, or whether there are unexplored factors driving their coevolution. Further progress in the development of life history theory is necessary and further empirical data from different primate lineages under different ecological settings, including primate genomics, transcriptomics, and proteomics, have to be compiled to convincingly identify targets of natural selection and to understand the full adaptive significance of life history variation among primates.

Differences in basic life history traits between species are suggested to be adaptive responses to past environments. As phylogenetic constraints they may limit growth and mortality patterns of extant primate populations and as a consequence affect their survival in rapidly changing environments. Most extant nonhuman primate species are now at risk of extinction. A better knowledge of their life history schedules and the limits of their phenotypic plasticity across distribution ranges along with information on their population dynamics and genetic variation may not only illuminate pathways for evolution but also help in establishing effective conservation and management programs. Since respective information on the link between distribution patterns, ecology, and life history is available for only a few species, comparative long-term field studies applying similar methodologies are urgently needed. These studies may also shed light on an interesting paradox in life history research, namely, that correlations for life history traits sometimes diverge in intra- and interspecific comparisons (Martin 2003).

Finally, understanding the peculiarities of human evolution will require further comparative research on nonhuman primates and their life histories. Thus, for instance, recent socioecological studies have unraveled an unexpected complexity in primate sociality, from solitary foraging and sleeping over dispersed or cohesive group-living to more flexible fission-fusion societies. Since these different degrees of sociality require quite different levels of brain complexity for spatial and social memory, integrative and comparative studies on life history, socioecology, communication, and cognition within and across the different primate lineages offer an excellent opportunity to illuminate our biological roots and the selective forces that shaped our own life history.

Appendix

See Table 1

Table 1 Primate database for life history traits compiled from the literature

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Cheirogaleidae	*Allocebus*	*trichotis*	83^{a}								
			78								
Cheirogaleidae	*Cheirogaleus*	*crossleyi*	294^{b}								
Cheirogaleidae	*Cheirogaleus*	*major*	356^{a}	1.15^{c}	71^{a}	1^{d}	2^{e}	∼18^{a}	70^{a}		15.0^{f}
			443		70		2–3		42		
					143^{g}						
Cheirogaleidae	*Cheirogaleus*	*medius*	139^{a}	1.2^{a}	62^{a}	12^{a}	2^{a}	12^{a}	61^{a}		9.0^{e}
			136		140^{g}	24			45		19
			282						66^{d}		
			169								
Cheirogaleidae	*Cheirogaleus*	*minusculus*	302								
Cheirogaleidae	*Cheirogaleus*	*sibreei*	∼262								
Cheirogaleidae	*Microcebus*	*berthae*	30^{a}								
			33								
Cheirogaleidae	*Microcebus*	*bongolavensis*	∼54								
Cheirogaleidae	*Microcebus*	*danfossorum*	∼63								
Cheirogaleidae	*Microcebus*	*griseorufus*	∼63^{h}	2^{i}	52	12^{i}	2^{i}				
			57								
Cheirogaleidae	*Microcebus*	*jollyae*	∼44								
			∼60								
Cheirogaleidae	*Microcebus*	*lehilahytsara*	45	1^{j}	57^{j}	3^{j}	2^{j}	4^{j}			15^{k}
Cheirogaleidae	*Microcebus*	*mamiratra*	∼61								
Cheirogaleidae	*Microcebus*	*mittermeieri*	∼44								
			∼40								
Cheirogaleidae	*Microcebus*	*murinus*	63^{a}	0.7^{l}	60^{a}	3^{m}	2^{a}	5^{a}	40^{a}	33^{k}	15.5^{e}
			∼62	1	62	12		∼6^{n}	55		9.0
			∼58						45		16.9^{o}
									49		
									33^{d}		

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Cheirogaleidae	*Microcebus*	*myoxinus*	~49[h]								
Cheirogaleidae	*Microcebus*	*ravelobensis*	56[a]	1[l]							9.0[l]
			62								
Cheirogaleidae	*Microcebus*	*rufus*	42[a]	1	57	12			40		
			44								
Cheirogaleidae	*Microcebus*	*sambiranensis*	44[a]								
			~44								
Cheirogaleidae	*Microcebus*	*simmonsi*	~65[p]								
Cheirogaleidae	*Microcebus*	*tavaratra*	61[a]								
			~61								
Cheirogaleidae	*Mirza*	*coquereli*	297[a]	1[a]	87[a]	12[a]	2[a]	14[a]	88[d]		15.3[q]
			299	2	91[d]			~16[n]			
				0.94[c]	89[r]						
					61[g]						
Cheirogaleidae	*Mirza*	*zaza*	299	1.9	89	7	1.6	~18			
Cheirogaleidae	*Phaner*	*electromontis*	~387								
Cheirogaleidae	*Phaner*	*furcifer*	328[a]								12.0[f]
Cheirogaleidae	*Phaner*	*pallescens*	351			24–36	1				
Cheirogaleidae	*Phaner*	*parienti*	~360								
Daubentoniidae	*Daubentonia*	*madagascariensis*	2,490[a]	3.5[a]	164[a]	20[a]	1[a]	102[a]	170[a]	1,535[a]	23.3[s]
			2,572[a]	2.29[c]	169[a]	30		147[a]	365[a]		32.0
					170				213		
					158				170		
					175[d]				150		
									548[d]		
									268[g]		
Lepilemuridae	*Lepilemur*	*aeeclis*	909								
Lepilemuridae	*Lepilemur*	*ahmansonorum*	~610								
Lepilemuridae	*Lepilemur*	*ankaranensis*	~790[t]								

Lepilemuridae	*Lepilemur*	*betsileo*	~1,150								
Lepilemuridae	*Lepilemur*	*dorsalis*	~730^{t}				1				
			798^{u}								
Lepilemuridae	*Lepilemur*	*edwardsi*	934^{a}		120–150^{v}		1^{v}				
			947^{v}								
Lepilemuridae	*Lepilemur*	*fleuretae*	~980								
Lepilemuridae	*Lepilemur*	*grewcockorum*	~940								
			~780								
Lepilemuridae	*Lepilemur*	*hubbardorum*	~990								
Lepilemuridae	*Lepilemur*	*jamesorum*	~780								
Lepilemuridae	*Lepilemur*	*leucopus*	594^{a}	1.7^{c}	61^{g}						8.6^{c}
Lepilemuridae	*Lepilemur*	*microdon*	~1,190^{t}								
Lepilemuridae	*Lepilemur*	*milanoii*	~720								
Lepilemuridae	*Lepilemur*	*mittermeieri*	~730								
Lepilemuridae	*Lepilemur*	*mustelinus*	~777^{a}	1.8^{a}	135^{a}	12^{d}	1^{q}	~27^{a}	75^{a}		12.0^{c}
			895^{u}		139^{d}		1^{u}		102^{d}		
			~1,000								
Lepilemuridae	*Lepilemur*	*otto*	~939								
Lepilemuridae	*Lepilemur*	*petteri*	600								
			585								
Lepilemuridae	*Lepilemur*	*randrianasoloi*	717								
Lepilemuridae	*Lepilemur*	*ruficaudatus*	779^{a}	1.6^{a}	176	12	1		120^{a}		10.0
			803		139^{d}				50		
Lepilemuridae	*Lepilemur*	*sahamalazensis*	787			12					
			679								
Lepilemuridae	*Lepilemur*	*seali*	~950								
Lepilemuridae	*Lepilemur*	*septentrionalis*	~750^{a}								
			~600–750								
Lepilemuridae	*Lepilemur*	*tymerlachsonorum*	~880				1				
Lepilemuridae	*Lepilemur*	*wrightae*	~950^{t}								
Lemuridae	*Eulemur*	*albifrons*	2,150	1.5	117	12			120		

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			1,950								
Lemuridae	*Eulemur*	*cinereiceps*	2,150[a]								
			2,140								
Lemuridae	*Eulemur*	*collaris*	2,217	2	120	12					
Lemuridae	*Eulemur*	*coronatus*	1,080[a]	2	125[a]	12	1[a]	48[a]			18.4[f]
			1,177[a]		120		1.5	~70[a]			
			~1,660		88[g]			~59[n]			
Lemuridae	*Eulemur*	*flavifrons*	2,290	3[w]		11.7[w]	1[w]		175[w]		
			2,170								
			1,760								
Lemuridae	*Eulemur*	*fulvus*	2,206[a]	2.2[a]	120[a]	24[a]	1[a]	68[a]	135[a]		37[f]
			2,250[a]	2.7[a]	123		1.1	76[a]	183[a]		22.5
			1,775		117			~72[n]	186[d]		
					125[g]				159[g]		
Lemuridae	*Eulemur*	*macaco*	1,760[a]	1.7[a]	129[a]	12[a]	1[a]	50[a]	135[a]		27.1[e]
			1,793[a]	2.2[a]	126	12.5		74[a]	70		36.2[x]
			2,148	2	128			~62[n]	139[d]		30.0[c]
			2,500	1.81[c]	124[d]						
			1,750								
			2,533								
			2,552								
			2,510								
Lemuridae	*Eulemur*	*mongoz*	1,481[a]	2.5[a]	129[a]	12	1[a]	57[a]	152[a]		24.3[f]
			1,560[a]	3	125			60[a]	63		25.3
			1,280	2.91[c]	137				157[d]		36.2[x]
			1,658		131[d]						30.0[c]
					126[r]						
					119[g]						
Lemuridae	*Eulemur*	*rubriventer*	1,940[a]	4.8	123[a]	12	1–2	82[a]	147–245		15.0

			1,960		126	24		∼86^{n}	110–135^{y}		20.0^{x}
									139^{d}		
Lemuridae	*Eulemur*	*rufifrons*	2,251	4	122^{o}	12			713^{o}		15.0
				3.4^{o}		27.4^{o}					33.6^{o}
Lemuridae	*Eulemur*	*rufus*	1,840								15.0
Lemuridae	*Eulemur*	*sanfordi*	∼1,852	2.55^{x}	120	12–24					25.0
			∼2,128								35.5^{x}
			∼2,030^{x}								
Lemuridae	*Hapalemur*	*alaotrensis*	∼1,450^{a}				1–2^{z}				
			∼1,239								
Lemuridae	*Hapalemur*	*aureus*	1,390^{a}		138	12^{a}			180		
			1,355								
Lemuridae	*Hapalemur*	*griseus*	670^{a}	2.4^{a}	140^{a}	11^{a}	1^{a}	∼45^{a}	120^{a}		12.1^{e}
			790^{a}	2.9^{a}	137	15.9		∼50^{n}	154^{a}		23.3^{x}
			915	3.3	143^{n}	12^{d}			131^{g}		
				2.68^{x}							
Lemuridae	*Hapalemur*	*meridionalis*	870								
Lemuridae	*Hapalemur*	*occidentalis*	1,188								
Lemuridae	*Prolemur*	*simus*	1,300^{a}		149	12.4			255		
			2,250		159^{r}						
Lemuridae	*Lemur*	*catta*	2,210^{a}	2.0^{a}	135^{a}	14^{a}	1^{a}	65^{a}	105^{a}		27.1^{e}
			2,290^{a}	2.3^{a}	136	12		85^{a}	179^{a}		21.0
			2,205	3	141			∼79^{n}	180		37.0
			1,760	3.2	139^{d}				60		
									183^{d}		
Lemuridae	*Varecia*	*rubra*	3,640		106	12	2.2		90–120		15.0 (LR)
			3,470		102						
Lemuridae	*Varecia*	*variegata*	3,100^{a}	1.42^{a}	102^{a}	32	2^{a}	78^{a}	89^{a}	2,893^{a}	28.0^{f}
			3,520^{a}	1.92^{a}	175^{a}	20		∼87^{a}	90^{a}		19.0

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			3,600[a]	2.72[a]	133[n]	12[d]		100[a]	146[a]		36.0[x]
			3,700	2.3					135		32.0[c]
			3,670	2.02[x]					180		
			3,517						150[d]		
			3,550								
			3,000								
			2,980								
Indriidae	*Avahi*	*betsileo*	1,050[aa]								
Indriidae	*Avahi*	*cleesei*	~860[aa]								
Indriidae	*Avahi*	*laniger*	~1,130[aa]	2.6[a]	157[d]	12[a]	1[q]		150[a]		
			1,320[a]						106[d]		
			1,200								
			1,307								
			1,050[ab]								
Indriidae	*Avahi*	*meridionalis*	1,200								
Indriidae	*Avahi*	*occidentalis*	777[a]		120		1[ac]				
Indriidae	*Avahi*	*peyrierasi*	~1,080								
			~1,110								
Indriidae	*Avahi*	*ramanantsoavanai*	1,019								
Indriidae	*Avahi*	*unicolor*	~840[aa]								
Indriidae	*Propithecus*	*candidus*	~6,300	4		20					
Indriidae	*Propithecus*	*deckenii*	2,630								
Indriidae	*Propithecus*	*coquereli*	3,244[a]	4.2[a]	141[a]	12[a]	1[a]	103[a]	182[a]		
			4,280[a]		162						
			3,757								
Indriidae	*Propithecus*	*coronatus*	~3,500–4,300		150						
Indriidae	*Propithecus*	*diadema*	6,260[a]	4[a]	178[a]	25[a]	1[q]	~135[a]	183[a]		
			6,508	4.5[a]	180	16.4			363[a]		
			4,930	4.26[x]	183[d]	24[d]			186[d]		

				5.3[o]		21.6[o]			479[o]		
Indriidae	*Propithecus*	*edwardsi*	5,895	4–6	179	19		∼165[ad]	180		32.0
			5,700	3.5[ad]							
			6,300								
Indriidae	*Propithecus*	*perrieri*	4,440								
			4,500								
Indriidae	*Propithecus*	*tattersalli*	3,500[a]	4.5[a]	180	12[d]		98[a]	153[a]		30.0
			3,590	4–5	186[d]				30		
									157[d]		
Indriidae	*Propithecus*	*verreauxi*	2,950[a]	3.5[a]	140[a]	12[q]	1[q]	103[a]	180[a]		18.2[q]
			3,620[a]	5	150–165	26.2			183		10.0
			2,766	4.04[x]	157[d]				195		30.5[x]
			3,122	2.59[c]	159[r]				186[d]		20.6[c]
			3,200								
Indriidae	*Indri*	*indri*	6,250[a]	4–7[ae]	159[a]	30[a]	1[q]		363[a]		
			6,840[a]	7–9	120–150	24–36			365		
			∼6,000–9,500		153[d]	24[d]			180		
					160[r]				248[d]		
Lorisidae	*Arctocebus*	*aureus*	∼210		131		1		100		4.0
					134[r]						
Lorisidae	*Arctocebus*	*calabarensis*	254[a]	1.12[a]	135[a]	6[a]	1[q]	32[a]	105[a]	160[a]	12.2[f]
			306[a]	0.82[c]	134	4.5			115		13.0[c]
			298		130				84		
			310								
Lorisidae	*Loris*	*lydekkerianus*	269[a]	1.45	162	14.8	1–2	∼12	169		
			181		167	6			145		
			180		160	6.6			148		
			275		163						
			260		164						
			238								
			193[a]								

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Lorisidae	*Loris*	*tardigradus*	255^{a}	1.5^{a}	166^{a}	6^{a}	1^{q}	10^{a}	170^{a}	139^{a}	16.0^{f}
			132	0.96^{c}	167		1–2	~11			23.0
					168						
Lorisidae	*Nycticebus*	*bengalensis*	950^{af}	2^{af}	187^{af}	12^{af}	1^{af}	38^{af}	180^{af}	525^{af}	15.0^{af}
			740	3	189	18			124		9.0
			890			15					
			1,400								
Lorisidae	*Nycticebus*	*coucang*	626^{a}	2.11^{a}	193^{a}	12^{a}	1^{a}	51^{a}	180^{a}	520^{a}	26.5^{f}
			637	1.5	191				90		18.0
					192				145		
					195^{g}				183		
Lorisidae	*Nycticebus*	*javanicus*	798^{a}								
			626								
Lorisidae	*Nycticebus*	*menagensis*	511^{a}				1				
Lorisidae	*Nycticebus*	*pygmaeus*	~307^{a}	3	185^{a}	24	2^{a}	20^{a}	108		9.0
			437		187		1–4		98		
			422		192^{r}				148		
			423								
Lorisidae	*Perodicticus*	*potto*	836^{a}	2.03^{a}	195^{a}	12^{a}	1^{a}	33^{a}	150^{a}		26.0^{f}
			1,572	1.54^{c}	197				120		9.0
			861		193						
			1,210^{a}								
Galagidae	*Euoticus*	*elegantulus*	283^{a}		135^{e}						
			~300								
Galagidae	*Euoticus*	*pallidus*	~300^{a}								
			~254								
Galagidae	*Galago*	*matschiei*	212^{a}								
			~210								
			~220								

Galagidae	*Galago*	*moholi*	173[a]	0.71[a]	123[a]	6[a]	1[a]	12[a]	84[a]	95[a]	16.5[q]
			179[a]	1[a]	124	4	2	15[a]	100[a]		14.0
			188	0.58				∼13[n]	45		
			185								
			151								
Galagidae	*Galago*	*senegalensis*	195[a]	1.4[a]	142[a]	6[a]	1[q]	19[ag]	98[a]	150[a]	16.0[e]
			200[ag]	1.02[ag]	141[ag]	5[ag]			84[ag]		13.0
			266			4–36			70–95		
Galagidae	*Galagoides*	*cocos*	137	1	120	4	1	∼16.5			
			148								
Galagidae	*Galagoides*	*demidovii*	60[ah]	0.97[a]	110[a]	12[a]	2[a]	8[a]	60[ah]		14.0[e]
			55		114[ah]		1	∼9[n]	53		12.0
Galagidae	*Galagoides*	*granti*	∼136								
			∼134								
			∼165								
Galagidae	*Galagoides*	*orinus*	∼90								
Galagidae	*Galagoides*	*rondoensis*	93								
			67								
Galagidae	*Galagoides*	*thomasi*	130[a]		110		1–2		42[ah]		10.0
			100[ah]								
			75								
Galagidae	*Galagoides*	*zanzibaricus*	132[a]	1[a]	126[a]	6[a]	1[q]	∼14[a]			
			∼127		124[r]						
			∼145								
Galagidae	*Otolemur*	*crassicaudatus*	1,110[a]	2.17[a]	135[a]	12[a]	2[a]	∼43[a]	135[a]	500[a]	18.8[f]
			1,250		133			∼45[n]	70		15.0
Galagidae	*Otolemur*	*garnettii*	721[a]	1.58[a]	132[a]	7[a]	1[a]	49[a]	140		15.0[f]
			805		130						
			1,027								
Galagidae	*Sciurocheirus*	*alleni*	262[a]	0.83[a]	135[a]	12[ai]	1[q]	24[a]	120[aj]		8.0[q]
			260[aj]		130[aj]		1[aj]	30[aj]			10.0[aj]
			∼432		133[r]						

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			∼276								
Galagidae	*Sciurocheirus*	*gabonensis*			133		1	∼24			
Tarsiidae	*Tarsius*	*bancanus*	109^{a}	2.52^{a}	178^{a}	8^{a}	1^{a}	$∼24^{a}$	79^{a}		12.0^{q}
			118	1		8.2		∼23	80		
			110	1.81^{c}		7.8		∼26	49		
			122			7.4		∼29			
			117			8.9		∼38			
			107								
			106								
Tarsiidae	*Tarsius*	*dentatus*	107^{a}				1^{a}				
			105								
Tarsiidae	*Tarsius*	*lariang*	102								
Tarsiidae	*Tarsius*	*pumilus*	52				1^{a}				
			58								
Tarsiidae	*Tarsius*	*sangirensis*	143								
			157								
Tarsiidae	*Tarsius*	*syrichta*	120^{a}		180^{a}		1^{a}	26^{e}	82^{a}		15.0^{f}
					178				68		
Tarsiidae	*Tarsius*	*tarsier* (*spectrum*)	108^{a}	1.42	191	5^{a}	1^{a}	$∼23^{a}$	68^{a}		12.0^{e}
			116	1.63^{c}		12.7			78		
			119								
Tarsiidae	*Tarsius*	*tumpara*	∼104								
Tarsiidae	*Tarsius*	*wallacei*	99								
Aotidae	*Aotus*	*azarae*	$1{,}230^{a}$	6.1^{ak}		12^{a}	1^{a}		231^{a}		
			1,240	5					150		
			1,246								
Aotidae	*Aotus*	*griseimembra*	923		133	13					
Aotidae	*Aotus*	*lemurinus*	874^{a}		133^{a}	12^{a}	1^{a}	98^{a}	75^{a}		
			859								

Aotidae	*Aotus*	*nancymaae*	780[a]								
Aotidae	*Aotus*	*nigriceps*	1,040[a]								
Aotidae	*Aotus*	*trivirgatus*	724[a]	2.38[a]	133[a]	9[q]	1[q]	94[a]	75[a]	360[a]	20.0[q]
			736[a]	2.42[a]		7.2[al]			179[a]		25.3[c]
			1,200	2.02[c]					76		
			~912[c]								
Aotidae	*Aotus*	*vociferans*	698[a]								
Aotidae	*Aotus*	*zonalis*	916								
Cebidae	*Cebus*	*albifrons*	2,067[a]	4.02[a]	155[a]	18[a]	1[q]	228[a]	269[a]	1,000[am]	44.0[q]
			2,228		160				273[an]		
					162[r]						
Cebidae	*Cebus*	*apella*	2,201[a]	5.5[a]	154[a]	22[a]	1[a]	197[a]	261[a]	1,000[a]	45.1[f]
			2,520[a]	5.78[a]	160	17.9[ao]		232[a]	264[a]		45.0
			3,000	6	157[r]				416[a]		46.0[x]
			2,300	3.5[al]					180		
				4.9[ao]							
Cebidae	*Cebus*	*capucinus*	2,540[a]	4[a]	162[a]	26[a]	1[a]	~230[a]	510[a]	1,350[a]	54.8[f]
			2,280	6.67	157			~250[o]	365		46.9
				5.85[c]							
Cebidae	*Cebus*	*flavius*	2,150								
			1,964								
Cebidae	*Cebus*	*kaapori*	2,150								
Cebidae	*Cebus*	*libidinosus*	1,975								
Cebidae	*Cebus*	*macrocephalus*	2,260		150						
Cebidae	*Cebus*	*nigritus*		7	151–155	19.35			360–540		38.4[o]
				6.7[o]		30.22			436[o]		
Cebidae	*Cebus*	*olivaceus*	2,520[a]	6[a]	155	26[q]	1[q]		730[a]		41.0
			2,395	6.92[c]	192[o]				365		
Cebidae	*Saimiri*	*boliviensis*	711[a]						719[an]		
			751								
			800								
Cebidae	*Saimiri*	*oerstedii*	680[a]			12	1[e]		120		

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			600						183^{an}		
Cebidae	*Saimiri*	*sciureus*	662^{a}	2.5^{a}	170^{a}	9^{a}	1^{a}	106^{a}	168^{a}	418	27.0^{f}
			699^{a}	3.9^{al}	171	13.6		146^{a}	183		21.0
			635						240^{a}		30.2^{x}
									330		
									243		
Cebidae	*Saimiri*	*ustus*	799^{a}								
			710								
Cebidae	*Saimiri*	*vanzolinii*	650^{a}								
Callitrichidae	*Callibella*	*humilis*	168								
Callitrichidae	*Callimico*	*goeldii*	355^{a}	1.32^{a}	151^{a}	9^{a}	1^{a}	48^{a}	65^{a}	215^{a}	17.9^{f}
			$\sim 582^{a}$	1.58	155^{a}	9.8		53^{a}	70^{a}		22.2^{x}
			523		150	5.5^{al}			150		
			536		152				112		
Callitrichidae	*Cebuella*	*pygmaea*	79^{a}	1.88^{a}	137^{a}	6^{q}	2^{a}	12^{a}	90^{a}	70^{a}	18.0^{f}
			122^{a}	2.25	142	5–7		14^{a}			10.0
			133	3		5^{al}					
Callitrichidae	*Callithrix*	*aurita*	429^{a}			5 (LR)	2				
			432								
Callitrichidae	*Callithrix*	*flaviceps*	$\sim 406^{a}$		150	7	2^{a}		28–58		5.0
			430			6.7					
			463								
Callitrichidae	*Callithrix*	*geoffroyi*	$\sim 359^{a}$		149^{ap}	7			56		
			190								
			370								
Callitrichidae	*Callithrix*	*jacchus*	287^{a}	1.37^{a}	148^{a}	6^{q}	2^{a}	27^{a}	60^{a}	128^{a}	16.7^{f}
			381^{a}	1.5^{a}	143	7.2		30^{a}	77^{a}		16.5
			360	2.91	144	5			90^{a}		22.8^{x}
			322	1.44^{x}		5.3			63^{al}		

				1.67^{an}							
Callitrichidae	*Callithrix*	*kuhlii*	∼375^{a}		140	5			42–70		
			∼350		143				56–77		
Callitrichidae	*Callithrix*	*penicillata*	307^{a}		150	5	2^{a}				
						5.3					
Callitrichidae	*Leontopithecus*	*caissara*	572^{a}			12			30		
			552								
Callitrichidae	*Leontopithecus*	*chrysomelas*	535^{a}	3.5	125	8.22					
			617								
			645								
Callitrichidae	*Leontopithecus*	*chrysopygus*			125						
Callitrichidae	*Leontopithecus*	*rosalia*	559^{a}	2.38^{a}	129^{a}	6^{a}	2^{a}	50^{a}	90^{a}	165^{a}	22.0^{f}
			598^{a}	2.42^{a}	125	10.37		62^{a}	84		14.0^{al}
			592	4.08		6.47			88^{an}		26.4^{o}
Callitrichidae	*Mico*	*acariensis*	420	3.0^{al}		10.0^{al}					
Callitrichidae	*Mico*	*argentatus*	353^{q}	1.67^{q}	150	7^{q}	2^{q}	36^{a}	120^{aq}		16.8^{f}
			355	1.92^{c}		6.5			28–56		16.5
Callitrichidae	*Mico*	*emiliae*	330^{a}								
Callitrichidae	*Mico*	*humeralifer*	380^{a}	1.6^{an}					91^{an}		15.0^{f}
Callitrichidae	*Mico*	*intermedius*	425			5					
Callitrichidae	*Mico*	*leucippe*	∼500								
Callitrichidae	*Mico*	*manicorensis*	135								
Callitrichidae	*Mico*	*mauesi*	398^{a}								
Callitrichidae	*Mico*	*melanurus*	380	1.67	150	6.3	2				
Callitrichidae	*Mico*	*nigriceps*	390^{a}				2^{a}				
			350								
Callitrichidae	*Mico*	*rondoni*	∼327								
Callitrichidae	*Mico*	*saterei*	413								
Callitrichidae	*Saguinus*	*bicolor*	430^{a}		160	6.5	2				8.0
Callitrichidae	*Saguinus*	*fuscicollis*	350^{a}	2.33^{a}	148^{a}	12^{a}	2^{a}	39^{a}	90^{a}		24.5^{f}
			296	2.73	150	6					10.5

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			404	2.42^{x}		6.2					24.9^{x}
			396	2.0^{al}		7.9^{al}					
			357								
Callitrichidae	*Saguinus*	*geoffroyi*	502^{a}		140–150	8^{q}	2^{a}	48^{a}			
			521			6–12					
			507								
Callitrichidae	*Saguinus*	*imperator*	475^{a}				2	47^{a}			20.2^{f}
			446								23.7^{x}
Callitrichidae	*Saguinus*	*inustus*	803^{a}								
Callitrichidae	*Saguinus*	*labiatus*	520^{a}		145^{a}	10^{a}	2^{a}	38^{a}			
			529								
			515								
Callitrichidae	*Saguinus*	*leucopus*	490^{a}					44^{a}			
Callitrichidae	*Saguinus*	*martinsi*									9.8
Callitrichidae	*Saguinus*	*midas*	558^{a}	2^{a}	140–168	7^{a}	2^{a}	40^{a}	70^{a}		13.0^{e}
			575		154^{r}	6.2			69		
						8					
Callitrichidae	*Saguinus*	*mystax*	539^{a}	1.25^{ar}	5^{ar}	11^{ar}	2^{a}	47^{a}	49		14.0
			554		150–160				90		
			579								
			593								
Callitrichidae	*Saguinus*	*niger*	505		140–168	8.4					7.5
			307								
Callitrichidae	*Saguinus*	*nigricollis*	350^{a}	2.33^{a}		8.3^{an}	1^{a}	44^{a}	77^{a}	175^{a}	15.2^{f}
			484^{a}				2		83^{a}		
			~447						60–90		
			~464						80^{al}		
Callitrichidae	*Saguinus*	*oedipus*	404^{a}	1.89^{a}	168^{a}	7^{q}	2^{a}	42^{a}	50^{a}	130^{a}	23.0^{f}
			420	1.92	183	12			40		20.0

			430		145[al]	9.2[al]			60		
			565						66[al]		
									80[an]		
Callitrichidae	*Saguinus*	*tripartitus*				10					
Pitheciidae	*Cacajao*	*ayresi*	3,100								
Pitheciidae	*Cacajao*	*calvus*	2,880[a]	3.6[as]	180[a]	24	1[as]		638[a]		22.3[f]
			3,600[a]	3.46[c]	185				640		20.0
									548[ab]		27.0[c]
Pitheciidae	*Cacajao*	*hosomi*	3,100								
Pitheciidae	*Cacajao*	*melanocephalus*	2,710[a]			24					18.0
			2,757								
Pitheciidae	*Callicebus*	*aureipalatii*	900								
Pitheciidae	*Callicebus*	*bernhardi*	~950								
Pitheciidae	*Callicebus*	*brunneus*	805[a]								
			850								
Pitheciidae	*Callicebus*	*caligatus*	~1,000								
Pitheciidae	*Callicebus*	*cinerascens*	~740								
Pitheciidae	*Callicebus*	*coimbrai*	1,215								
Pitheciidae	*Callicebus*	*cupreus*	1,120[a]		130[a]	13[a]	1[a]	74[a]	203[a]		
			825								
Pitheciidae	*Callicebus*	*discolor*	1,075								
Pitheciidae	*Callicebus*	*donacophilus*	909[a]								
Pitheciidae	*Callicebus*	*hoffmannsi*	1,030[a]								
Pitheciidae	*Callicebus*	*lucifer*				12			120 (LR)		
Pitheciidae	*Callicebus*	*lugens*	1,050								
			1,260								
Pitheciidae	*Callicebus*	*medemi*	1,310								
Pitheciidae	*Callicebus*	*melanochir*	1,370								
Pitheciidae	*Callicebus*	*moloch*	956[a]	3[a]	164[a]	12[q]	1[q]	74[a]	60[a]		12.0[q]
			877	3.46[c]	129[r]						26.2[x]
Pitheciidae	*Callicebus*	*oenanthe*				9.3			150–201		
Pitheciidae	*Callicebus*	*ornatus*	1,163								

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Pitheciidae	*Callicebus*	*pallescens*	~800								
Pitheciidae	*Callicebus*	*personatus*	1,380[a]				1[as]				
			1,378								
Pitheciidae	*Callicebus*	*purinus*	~1,500								
			~1,200								
Pitheciidae	*Callicebus*	*stephennashi*	668								
Pitheciidae	*Callicebus*	*torquatus*	1,210[a]	4[s]		12[aq]	1[as]		139[ab]		
Pitheciidae	*Chiropotes*	*albinasus*	2,490[a]		152[as]				90		11.7[f]
			2,518		150						
Pitheciidae	*Chiropotes*	*chiropotes*	2,400								
			2,600								
Pitheciidae	*Chiropotes*	*satanas*	2,580[a]		152[as]						15.0[f]
			3,100[a]								
			2,500								
Pitheciidae	*Pithecia*	*aequatorialis*	~2,250[a]								
Pitheciidae	*Pithecia*	*albicans*	~2,200								
Pitheciidae	*Pithecia*	*irrorata*	2,070[a]								
Pitheciidae	*Pithecia*	*monachus*	2,110[a]		165	24		120[a]	240		24.6[f]
			1,895						365		
			1,900								
Pitheciidae	*Pithecia*	*pithecia*	1,580[a]	2.08[a]	164[a]	19[q]	1[q]		150		13.7[e]
			1,611	6.33	146	21			110[ab]		20.7[c]
			1,500	2.98[c]							
			1,515								
			1,512								
Atelidae	*Alouatta*	*arctoidea*		5.17	191						
				4							
Atelidae	*Alouatta*	*belzebul*	5,520[a]								
			4,450								

Atelidae	*Alouatta*	*caraya*	4,330[a]	3.71[a]	187[a]	15.9	1[q]	262[a]	325[a]		26.0
			4,882[a]	4.5	152–195						
			4,900	3.5[c]							
			4,840								
			4,400								
Atelidae	*Alouatta*	*guariba*	4,350		190	21.2					
Atelidae	*Alouatta*	*macconnelli*	5,210								
			6,020								
Atelidae	*Alouatta*	*palliata*	4,020[a]	3.58[a]	186[a]	20[a]	1[a]	320[a]	325[a]	1,100[a]	13.0[e]
			5,350[a]	3.99[a]		22		~460[o]	495[a]		25.0[c]
			5,824[a]	3.75[al]		25.0[at]			630[a]		21.0[o]
			6,600[a]						502		
			4,855								
Atelidae	*Alouatta*	*pigra*	6,430[a]	4	183			~480[a]			
			5,608		184						
Atelidae	*Alouatta*	*seniculus*	4,670[a]	4.58[a]	191[a]	17[q]	1[q]	295[a]	372[a]		25.0[q]
			6,020[a]	5.2[o]	195[o]	16.6			335[o]		19.8[o]
			5,600								
			4,034								
			6,298								
Atelidae	*Alouatta*	*ululata*	~4,700								
Atelidae	*Ateles*	*belzebuth*	7,850[a]			24	1				
			7,880								
			8,112								
Atelidae	*Ateles*	*chamek*	9,330[a]			34.5					
			~7,000								
Atelidae	*Ateles*	*fusciceps*	9,160[a]	4.86[a]	226[a]	27[q]	1[q]		486[a]		24.0[f]
			8,800	4.88		36.5			365		20.0
			9,163	4.25		26			480		
			9,100								
Atelidae	*Ateles*	*geoffroyi*	7,290[a]	5.62[a]	225[a]	37[a]	1[a]	426[a]	750[a]	2,000[a]	48.0[f]

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			7,669[a]	6.39[a]	229[a]	31.9		∼512[a]	821[a]		23.0
			6,624	7.08	226–232	34.7			791		27.3[c]
			7,456						730		41.0[o]
Atelidae	*Ateles*	*hybridus*	∼4,000								
Atelidae	*Ateles*	*marginatus*	5,824								
Atelidae	*Ateles*	*paniscus*	8,440[a]	5[a]	230[a]	24[a]	1[a]	425[a]	760[a]	3,790[a]	33.0[q]
			8,554[a]	5.8[c]		46		480[a]	810[a]		37.8[c]
									821		
Atelidae	*Brachyteles*	*arachnoides*	8,070[a]	7.5[a]	233[a]	34[a]	1[a]		638[a]		30.0
			9,450		216	24			855[a]		
									365		
									913[ab]		
Atelidae	*Brachyteles*	*hypoxanthus*	8,400	9.88	216	36.5			365		30.0
				7.17					450		
Atelidae	*Lagothrix*	*cana*	6,400								
			7,650								
Atelidae	*Lagothrix*	*lagotricha*	5,585[a]	5[a]	223[a]	24[a]	1[a]	432[a]	315[a]		30.0[f]
			7,020[a]	7.58[a]	225[a]	18–24		447[a]	507[a]		21.0[o]
			5,740	4.74[c]		12–24			240		
			5,706	9[o]		36.7[o]			610[ab]		
Atelidae	*Lagothrix*	*lugens*	5,750	9	225	36.7			365		30.0
			6,000								
Atelidae	*Oreonax*	*flavicauda*	∼10,000[a]								
Cercopithecidae	*Allenopithecus*	*nigroviridis*	3,180[a]					242[a]			
			3,700								
Cercopithecidae	*Miopithecus*	*ogouensis*	1,100	4.46	165	12		∼200	365		28.0
			1,080	4	167	6.5					
			1,120								
Cercopithecidae	*Miopithecus*	*talapoin*	1,120[a]	4.38[a]	162[a]	12[a]	1[a]	∼178[a]	180[a]	450[a]	30.9[f]

			2,000[a]	4.75[c]	165[a]			180[a]	195[a]		
Cercopithecidae	*Erythrocebus*	*patas*	6,317[a]	3[a]	167[a]	12[a]	1[a]	468[a]	213[a]	1,950[a]	23.9[f]
			6,500[a]	3.09		12.9		625[a]	255[a]		28.3[x]
				3.41[c]		14.4			365		
						13.8[al]			222[al]		
Cercopithecidae	*Chlorocebus*	*aethiops*	2,980[a]	4.75[a]	163[a]	12[a]	1[a]	336[a]	219[a]	1,170[a]	31.0[e]
			3,100[a]	5[a]	165	13.3		430[a]	201[a]		26.5[o]
			2,740	3.5[a]		11.8			365[a]		
			2,570	5.1		16.8			252		
			3,300								
Cercopithecidae	*Chlorocebus*	*pygerythrus*	2,570	2.83	165	20.4			270–540		31.0
			3,200	5.1	163	16.8			300–540		
			2,740	5		13.3			300–330		
Cercopithecidae	*Chlorocebus*	*sabaeus*	3,300			11.8			252		30.0
			4,960								
			3,450								
			4,400								
Cercopithecidae	*Cercopithecus*	*ascanius*	2,920[a]	5[a]	172[a]	52[q]	1[q]	~371[a]	180[e]		28.3[f]
			2,901	4–5	162 (LR)	17.95			730		28.25
			2,790			24.7					
			3,300			53.7					
Cercopithecidae	*Cercopithecus*	*campbelli*	2,200[a]	3[au]	180	12[au]			365[a]		
			2,700[a]								
			3,600								
Cercopithecidae	*Cercopithecus*	*cephus*	2,805[a]	5[a]	170[a]	27.4	1[q]	339[a]	366[q]		22.0[q]
			2,800	4.17[c]							23[c]
			2,900								
Cercopithecidae	*Cercopithecus*	*diana*	3,900[a]	5.33[a]		12[a]	1[a]	460[a]	365[a]		37.3[f]
			4,533[a]	5.42[a]				479[a]			34.8
			2,260	6.25[c]							
Cercopithecidae	*Cercopithecus*	*dryas*	2,250								
Cercopithecidae	*Cercopithecus*	*erythrogaster*	2,400[a]								

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Cercopithecidae	*Cercopithecus*	*erythrotis*	~2,900[a]				1[e]		180[e]		16.0
			2,300								
Cercopithecidae	*Cercopithecus*	*hamlyni*	3,360[a]					~280	240		27.0[f]
			3,061								12.7
			3,680								
Cercopithecidae	*Cercopithecus*	*lhoesti*	3,450[a]	5.77	180	16[q]	1[q]				15.46
			4,700[a]			7.73					
Cercopithecidae	*Cercopithecus*	*mitis*	3,930[a]	5.72[a]	140[au]	24[a]	1[a]	~337[a]	692[a]		20.0[q]
			4,910[a]	5.92	176	13.5		495[a]	480		29.0
			4,250	5.42		18		~402	900		37.8[x]
			4,280	6.5		19.2		~700	183		
			4,600			47			699		
			2,758			29					
			3,929								
			4,240								
Cercopithecidae	*Cercopithecus*	*mona*	2,500[a]	3.22	158		1[e]	282[a]			22.0[f]
			3,100								22.5
			3,000								
			3,700								
Cercopithecidae	*Cercopithecus*	*neglectus*	3,550[a]	4.67[a]	165[a]	12[a]	1[a]	260[a]	365[a]	1,640[a]	20.0[e]
			4,081[a]	3.54	168	14.3		450[a]	420[a]		22
			3,190	5		23					30.8[x]
				5.69[c]		13.1					
Cercopithecidae	*Cercopithecus*	*nictitans*	4,216[a]	4[au]	170[a]		1[e]	406[a]			
			4,200	4.7							23.0[c]
			4,410								
			4,092								
			3,650								
Cercopithecidae	*Cercopithecus*	*petaurista*	2,900[a]								19.0[f]

			2,275								
			2,356								
Cercopithecidae	*Cercopithecus*	*pogonias*	2,900[a]	5[a]	170[a]	21.1	1[a]	339[a]			20.0[q]
			3,550	4.62[c]	168			~435[a]			19.0
			2,940								24.1[c]
			2,870[a]								
			2,880								
Cercopithecidae	*Cercopithecus*	*preussi*	~4,500[a]								
			~7,000								
Cercopithecidae	*Cercopithecus*	*sclateri*	~2,500[a]								
			3,800								
Cercopithecidae	*Cercopithecus*	*solatus*	3,920[a]	4.75[a]		18[a]	1[a]				
			3,900								
Cercopithecidae	*Macaca*	*arctoides*	8,400[a]	3.84[a]	178[a]	19[a]	1[a]	489[a]	393[a]	2,300[a]	30.0[e]
				4	177	19.32			291		
				3.5[av]		23.5[av]					
Cercopithecidae	*Macaca*	*assamensis*	6,900[a]	5[aw]	164[aw]	13.9[aw]					
			6,700			23.2[aw]					
			7,800								
			8,750								
			10,300								
Cercopithecidae	*Macaca*	*cyclopis*	4,940[a]	4	162[a]	15[a]	1[a]	398[a]	206[a]		
			6,200[a]		165[r]	13.4		402[a]	365		
			6,690								
Cercopithecidae	*Macaca*	*fascicularis*	3,574[a]	3.9[a]	160[a]	13[a]	1[a]	326[a]	330[a]	1,700[a]	37.1[s]
			3,590[a]	5.17	167[a]	29.3		375[a]	420[a]		31.0
			3,000	5.23	164						39.0[x]
			3,020	3.86	162						
			3,100		165						
Cercopithecidae	*Macaca*	*fuscata*	8,030[a]	5.54[a]	173[a]	24[a]	1[a]	503[a]	365[a]	2,730[a]	33.0[s]

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			$9,100^{a}$	7.05	176	18		527^{a}	540^{a}		38.5^{x}
			8,800	6.1		19.1					
						17.5^{av}					
Cercopithecidae	*Macaca*	*hecki*	6,800								
Cercopithecidae	*Macaca*	*leonina*	4,400–5,700		171						
Cercopithecidae	*Macaca*	*maura*	$6,050^{a}$	5^{a}	163^{e}	22^{a}	1^{a}	389^{a}	500^{a}		28.0
			5,100	6.5^{ax}	176	29^{ax}					
			5,565	6–7	174^{r}	22.4					
Cercopithecidae	*Macaca*	*mulatta*	$5,370^{a}$	3^{a}	165^{a}	12^{a}	1^{a}	466^{a}	192^{a}	$1,454^{a}$	36.0^{f}
			$6,500^{a}$	4.5^{a}	167^{r}				365^{a}		29.0
			$8,800^{a}$	3.9^{x}					264		40.0^{x}
			5,340	5.0^{av}							31.0^{o}
Cercopithecidae	*Macaca*	*munzala*	~15,000			24					
Cercopithecidae	*Macaca*	*nemestrina*	$4,900^{a}$	3.92^{a}	167^{a}	14^{a}	1^{a}	444^{a}	234^{a}	$1,320^{ay}$	26.3^{e}
			$5,571^{a}$	4.5^{av}	171^{a}	13.5		473^{a}	365^{a}		37.6^{x}
			$6,500^{a}$		170						34.3^{c}
			5,400		175						
			6,480								
Cercopithecidae	*Macaca*	*nigra*	$4,600^{a}$	5.44^{a}	170^{a}	18^{a}	1^{a}	457^{a}			18.0^{e}
			$5,470^{a}$	5.5^{a}	174			$\sim 461^{a}$			
				5.42							
Cercopithecidae	*Macaca*	*nigrescens*	5,500								
Cercopithecidae	*Macaca*	*ochreata*	$2,600^{a}$								
			7,500								
			6,388								
Cercopithecidae	*Macaca*	*radiata*	$3,700^{a}$	4^{a}	162^{a}	12^{a}	1^{a}	388^{a}	365^{a}	$2,000^{a}$	30.0^{q}
			3,740	4.5^{az}	166^{az}	12.7			180		
			3,670	3	150	15.29					
			3,850								

Cercopithecidae	*Macaca*	*siberu*	~5,950								
Cercopithecidae	*Macaca*	*silenus*	5,000[a]	4.92[a]	180[a]	17[a]	1[a]	407[a]	365[a]		38.0[q]
			6,100	6	170	23.18			450		40.0[x]
				6.6[av]	172[r]	30					
Cercopithecidae	*Macaca*	*sinica*	3,200[a]	5[q]	167	18[q]	1[q]				30.0[q]
			3,066	6.02		12.3			180–420		36.0
				4.8[av]		17.3					
						19.1[av]					
Cercopithecidae	*Macaca*	*sylvanus*	8,280[a]	4.75[a]	165[a]	22[a]	1[a]	450[a]	210[a]	2,420[a]	22.0[q]
			~11,000[a]	3.83		13–31			180		
			10,200								
Cercopithecidae	*Macaca*	*thibetana*	9,500[a]	5.5	170[a]	24[a]	1[a]	500[a]	561[a]	2,400[a]	20.0
			12,800[a]	5	240	15.2		~550[a]	568[a]		
				5.4		16.3			180		
						15.7			210		
Cercopithecidae	*Macaca*	*tonkeana*	9,000[a]	5	176						
			7,270		173[r]						
Cercopithecidae	*Mandrillus*	*leucophaeus*	8,450[a]	5[a]	173[a]	15[q]	1[q]	722[a]			28.6[e]
			~12,500[a]	4.52	176	39.4					33.4[c]
			11,600		179[r]						
			8,500								
Cercopithecidae	*Mandrillus*	*sphinx*	11,350[a]	4[a]	175[a]	17[a]	1[a]	613[a]	348[a]	3,000[a]	29.1[e]
			12,900[a]	4.33	220[a]	12.4		890[a]	350[a]		47.0
			8,957	5.8[c]	167	13			240		
			10,000								
Cercopithecidae	*Cercocebus*	*agilis*	5,660[a]		180	21 (LR)			180		
			5,405		168						
Cercopithecidae	*Cercocebus*	*atys*	6,200[a]	3.14[q]	167[e]	13[q]	1[q]	530[a]			26.8[f]
			5,500	3.62[c]	152	12					21.0
			6,400								
Cercopithecidae	*Cercocebus*	*chrysogaster*	8,000	4.9	174	19.9					

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Cercopithecidae	*Cercocebus*	*galeritus*	$5,260^{a}$	6.5^{a}	171^{a}	18–24	1^{q}		180–300		19.0^{e}
			3,700	7.5^{c}	180						21.0^{c}
				3.6^{c}							
Cercopithecidae	*Cercocebus*	*torquatus*	$5,500^{a}$	4.67^{a}	171^{a}	13^{q}	1^{q}				27.0^{q}
			5,800	3.33	213	16.1					30.0^{c}
			8,500	6.5		19.1					
			6,230	4.5							
			5,100	3.44							
			6,560								
Cercopithecidae	*Lophocebus*	*albigena*	$6,020^{a}$	4.08^{a}	186^{a}	33^{a}	1^{a}	500^{a}	210^{a}	$2,200^{ay}$	32.7^{q}
			$6,209^{a}$	7.3	175^{a}	25^{q}	1^{q}	500^{3}	365^{a}	$2,170^{a}$	
			4,000–7,000	6.92^{c}	183	33.33					
Cercopithecidae	*Lophocebus*	*aterrimus*	$5,760^{a}$								26.8^{f}
			5,640								
Cercopithecidae	*Rungwecebus*	*kipunji*	~10,000								
Cercopithecidae	*Papio*	*anubis*	$11,700^{a}$	4.5^{a}	180^{a}	25^{a}	1^{a}	915^{a}	584^{a}	$3,800^{am}$	25.2^{f}
			$13,300^{a}$	6.92	186	30.3		950^{a}	600^{a}		19.7
			$14,700^{a}$	6.32	185	22.2			420		48.0
			12,200		182^{r}	25.2			304		
			12,280			23.5					
			14,000			15					
			12,800			29.9					
						16.5					
						13.8^{al}					
Cercopithecidae	*Papio*	*cynocephalus*	$9,750^{a}$	5.5^{a}	173^{a}	23^{a}	1^{a}	710^{a}	365^{a}	$2,500^{a}$	40.0^{q}
			$11,000^{a}$	7.02^{c}	175^{a}	21		803^{a}	450^{a}		14.65
			$11,532^{a}$		182	27.94			456^{a}		45.0^{c}
			$13,600^{a}$						360		
			10,358								

			10,920								
			15,900								
Cercopithecidae	*Papio*	*hamadryas*	9,900[a]	6.1[a]	170[a]	24[a]	1[a]	695[a]	561[a]	3,100[a]	37.5[f]
			10,404[a]	4.4	181	18.8		1,000[a]	450[al]		30.0
			11,400[a]	6.08	172[al]	12					35.6[al]
						22					
Cercopithecidae	*Papio*	*papio*	12,100[a]	4.25	187[a]	14[q]	1[e]	604[a]			40.0[q]
			16,166[a]		182[r]						23.0
			12,000								37.5[x]
Cercopithecidae	*Papio*	*ursinus*	14,773[a]	3.67[a]	187[a]	29[a]	1[a]	600[a]	480 (HR)		45.0[q]
			14,800[a]	6.75	180	27.7		850[a]			13.91
			15,700			25					
			16,800			38					
						24.6					
Cercopithecidae	*Theropithecus*	*gelada*	11,427[a]	4[a]	170[a]	24[a]	1[a]	465[a]	540[a]	3,900[a]	28.0[f]
			11,900[ab]	4.5[al]	182	26			450[al]		
				5.19[c]		38					
						17.2[al]					
Cercopithecidae	*Procolobus*	*gordonorum*				34.4					
Cercopithecidae	*Procolobus*	*kirkii*	6,800			34	1				
						41					
Cercopithecidae	*Procolobus*	*pennantii*	~8,300								
Cercopithecidae	*Procolobus*	*preussi*	~8,300								
Cercopithecidae	*Procolobus*	*rufomitratus*	7,500	5	135	27.5			673		8.75
			7,000			24.5			450		
Cercopithecidae	*Procolobus*	*verus*	4,200[a]		180	19.2	1[e]				
			3,500		155–186[ba]						
Cercopithecidae	*Procolobus*	*badius*	7,421[a]	4.08[a]	153–159	25[q]	1[q]		522[a]		
			8,210[a]	4,17		29.4			790[a]		
			8,200						270–730		
Cercopithecidae	*Colobus*	*angolensis*	7,570[a]		195	15	1[e]		365		22.3[s]
			7,400		168						36.0

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
Cercopithecidae	*Colobus*	*guereza*	7,900[a]	4.75[a]	170[a]	20[a]	1[a]	445[a]	330[a]	1,600[a]	24.5[f]
			8,102[a]	4.5	152	22		549[a]	390[a]		23.75
			9,200[a]	5.28[c]	158	17			394[a]		35.0[x]
			8,237			12			334		
						25[a]					
Cercopithecidae	*Colobus*	*polykomos*	7,662[a]	8.5[a]	170[a]	22[a]	1[a]	400[a]	215[a]	1,240[a]	30.5[f]
			8,300[a]	4.46[c]	186[ba]	24		∼600[a]	219[a]		
Cercopithecidae	*Colobus*	*satanas*	7,420[a]		195[e]		1[e]		480[e]		
			9,500			24					
			10,400								
Cercopithecidae	*Colobus*	*vellerosus*	6,900[a]								
Cercopithecidae	*Semnopithecus*	*ajax*		6.7[ba]	209[ba]	28.8[ba]			759[ba]		
Cercopithecidae	*Semnopithecus*	*dussumieri*	11,700								
Cercopithecidae	*Semnopithecus*	*entellus*	6,910[a]	3.42[a]	184[a]	17[a]	1[a]	500[a]	249[a]	2,100[a]	25.0[s]
			9,890[a]	3.9[a]	200[a]	16.7			396[a]		30.0
			10,280[a]	3.54	209	28.8			416[a]		18.3[o]
			14,800[a]	6.7	212[r]	25.3[ba]			384		
			11,700						747		
			8,500								
			16,100								
			12,300								
			9,510								
Cercopithecidae	*Semnopithecus*	*schistaceus*	12,320			20–24[ba]					
			16,100								
Cercopithecidae	*Trachypithecus*	*auratus*	∼7,100								
Cercopithecidae	*Trachypithecus*	*barbei*	6,400								
Cercopithecidae	*Trachypithecus*	*cristatus*	5,760[a]	4[a]	180	16.75	1[e]		365[a]		31.1[f]
			5,700	2.88	195	14.9					
						15.4[av]					

Cercopithecidae	*Trachypithecus*	*delacouri*	7,800	6.42					350		18.0
Cercopithecidae	*Trachypithecus*	*francoisi*	7,300[a]	4[a]	184	19.1		457[a]	394[a]		20.0
			6,690	5.42		16			132		
			7,200						400		
			4,950								
Cercopithecidae	*Trachypithecus*	*geei*	9,500[a]	4.92	180	18.5	1[e]		451		
Cercopithecidae	*Trachypithecus*	*hatinhensis*	7,200	5.42		27.6			400		17.0
Cercopithecidae	*Trachypithecus*	*johnii*	11,200[a]			22	1[e]		305–336[ba]		
			10,900								
Cercopithecidae	*Trachypithecus*	*laotum*	~9,600								
Cercopithecidae	*Trachypithecus*	*obscurus*	6,260[a]	4[a]	150[e]		1[e]	341[a]	365[a]		25.0[f]
			6,530[a]					485[e]			
			6,470								
			6,000								
Cercopithecidae	*Trachypithecus*	*phayrei*	6,300[a]	5.3[av]	165[a]	15[a]	1[a]		305[a]		
			10,500[a]		205[a]	22.3[av]			310		
			6,400								
Cercopithecidae	*Trachypithecus*	*pileatus*	9,860[a]	4	180	18	1[bb]		458[bc]		35.0
					200[bb]	23[bb]			430		
Cercopithecidae	*Trachypithecus*	*poliocephalus*	8,700	2.83	214	25[av]	1[ba]		200		
			7,820	5.4[av]	210				365		
			7,800						579–640[bd]		
Cercopithecidae	*Trachypithecus*	*vetulus*	5,797[q]	3.8[aq]	195[be]	20[q]	1[q]	360[3]	214[q]	1,100[am]	23.0[f]
			5,900[a]	4[a]	200[a]	32[a]		~447[a]	219[a]		26.1
			5,684	3.92–4.67	270	24			270[a]		
				3.05[c]	198[av]				30–180		
Cercopithecidae	*Presbytis*	*comata*	6,710[a]								
Cercopithecidae	*Presbytis*	*femoralis*							275–305[ba]		
Cercopithecidae	*Presbytis*	*frontata*	5,670[a]								
			~5,620								
Cercopithecidae	*Presbytis*	*hosei*	5,630[a]	3					300		

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			5,570								
			6,000								
Cercopithecidae	*Presbytis*	*melalophos*	6,470[a]	3.8[aq]			1[e]				16.0[f]
			6,600[ab]								
Cercopithecidae	*Presbytis*	*potenziani*	6,400[a]				1[e]				
Cercopithecidae	*Presbytis*	*rubicunda*	6,170[a]			12 (LR)	1[e]		470 (LR)		
			6,040								
			6,000								
Cercopithecidae	*Presbytis*	*siamensis*	7,100								
			7,300								
			5,400								
			6,300								
Cercopithecidae	*Presbytis*	*thomasi*	6,690[a]	5.4		22			579		20.0
			7,500			26.8[av]			634[o]		
Cercopithecidae	*Nasalis*	*larvatus*	9,593[a]	4.5[a]	166[a]	18[a]	1[a]	450[a]	210[a]	2,000[a]	21.0[f]
			10,000	5		24			281[a]		25.1
			9,033	5.2[c]							
			10,500								
			9,900								
Cercopithecidae	*Simias*	*concolor*	6,800[a]				1[bf]				
			7,100								
Cercopithecidae	*Pygathrix*	*nemaeus*	8,180[a]	4.83	210[a]	20[q]	1[q]	463[a]	176		10.3[q]
			9,980		191	22			336[ab]		30.0
Cercopithecidae	*Pygathrix*	*nigripes*	8,700								
			9,007								
Cercopithecidae	*Rhinopithecus*	*avunculus*	8,000[a]								
			8,500								
Cercopithecidae	*Rhinopithecus*	*brelichi*		8.6[ba]		38.2[ba]					
Cercopithecidae	*Rhinopithecus*	*bieti*	9,960[a]	5.5	204	16.7		427[a]			

			9,100		196	20.8					
			8,900			23.2[av]					
			8,200			36[ba]					
Cercopithecidae	*Rhinopithecus*	*roxellana*	11,600[a]	5	202	23.3[av]			275–336[ba]		
			8,428	5.6[av]	195[r]	21.9[ba]					
			8,450								
Hylobatidae	*Hoolock*	*hoolock*	6,880[a]	5.99[aq]		36	1[e]		700[e]		
			6,100								
Hylobatidae	*Hylobates*	*agilis*	5,820[a]	8	210	24	1[e]		724[aq]		
			6,400						730		
									720		
Hylobatidae	*Hylobates*	*albibarbis*							720		
Hylobatidae	*Hylobates*	*klossii*	5,920[a]	9.07[aq]	210[e]	40[bg]			330[e]		
			5,890								
Hylobatidae	*Hylobates*	*lar*	5,340[a]	6.69[a]	205[a]	30[a]	1[a]	400[a]	548[a]	1,070[a]	31.5[e]
			5,465[a]	9.31[a]	213[a]	43		407[a]	730[a]		40.0
			5,300	11.17	240	41[bh]			840		52.0[x]
				8.0[x]					671[bh]		
				7.5[al]							
Hylobatidae	*Hylobates*	*moloch*	5,292[a]		195[a]		1[e]		724[aq]		
			6,250								
Hylobatidae	*Hylobates*	*muelleri*	5,350[a]	7.08	210	24					57.0
			6,400	8	195[r]						
			5,250								
Hylobatidae	*Hylobates*	*pileatus*	5,440[a]	6.7[c]							36.0[f]
Hylobatidae	*Nomascus*	*concolor*	5,749[a]	7[aq]	202[a]		1[e]		724[aq]		44.1[f]
			7,620[a]	6.7[c]							25.0
			~5,000								
			~6,900								
Hylobatidae	*Nomascus*	*gabriellae*	5,233		200–212	20.1		~500			
Hylobatidae	*Nomascus*	*hainanus*	6,563	6	173	24.5			540–729		
Hylobatidae	*Nomascus*	*leucogenys*	7,320[a]		210			500[a]			45.0

(*continued*)

Table 1 (continued)

Family	Genus	Species	BM	AFR	GL	IBI	LS	NNM	WA	WM	L
			6,600		202^{r}						
			7,000								
Hylobatidae	*Nomascus*	*siki*	7,867	8.83	200–212						44.0
				7.5							
Hylobatidae	*Symphalangus*	*syndactylus*	10,568^{a}	5.18^{a}	232^{a}	50^{a}	1^{a}	513^{a}	639^{a}	3,500^{bi}	37.0^{f}
			10,700	9^{a}	230	31.2			332		43.0^{x}
				8	210	33.7			365		
				7.7^{x}	234^{r}						
Hominidae	*Pongo*	*pygmaeus*	35,700^{a}	7^{a}	250^{a}	72^{a}	1^{a}	1,728^{a}	720^{a}	11,000^{a}	58.8^{f}
			37,078^{a}	14.3^{a}	245	92			1,825^{a}		50.0^{al}
			35,800	15.67	254^{r}	84			2,008		
			38,800	10.32^{x}	260^{al}	73.2			1,095^{al}		
						33.6^{al}					
Hominidae	*Pongo*	*abelii*	35,600^{a}	15.4^{bj}	245	112^{bj}		1,653^{o}	2,555		58.0^{bj}
			38,300	13.5^{o}		98.4			2,318^{o}		45.5^{o}
						111.6					
Hominidae	*Gorilla*	*gorilla*	71,000^{a}	4^{a}	260^{a}	47^{a}	1^{a}	1,996^{a}	900^{a}	19,800^{am}	54.0^{f}
			71,500^{a}	10.0^{a}	285^{a}	48		2,110^{a}	1,004^{a}		39.3^{al}
			80,000^{a}	10.3^{a}	257^{r}				1,278^{a}		
			97,500^{a}	8.1^{x}					1,679		
				7.3^{bk}					1,583^{al}		
				9.85^{al}							
Hominidae	*Gorilla*	*beringei*	97,500	9.92	255	42			1,583		40.0
			93,000	10	258	48			1,177^{o}		
			55,000	10.58		46.8					
						55					
Hominidae	*Pan*	*paniscus*	33,200^{a}	13–15^{bl}	240^{a}	48^{a}	1^{a}	1,400^{a}	1,080^{a}	8,500^{a}	26.8^{q}
			33,000	13	231	28			1,095		40.0
			32,000			60			1,460		55.0^{x}

			31,000			72					44.0[o]
Hominidae	*Pan*	*troglodytes*	30,000[a]	13[a]	235[a]	60[a]	1[a]	1,750[a]	1,680[a]	8,500[a]	59.4[f]
			33,700[a]	13.9[a]	240[a]	62		1,814[a]	1,702[a]		50.0
			45,800[a]	15.58	225	72.5			1,460		
			31,300	12.58	232	63			1,702		
			35,200	10.9	228[al]	68			1,965		
			50,000	13.7		58.8			1,922		
			43,800	11.7[bk]		69.1					
			41,600								
Hominidae	*Homo*	*sapiens*	42,200[a]	14[a]	267[a]	36[a]	1[a]	2,900[a]	730[a]	10,980[a]	120.6[f]
			45,800[a]	15[a]	270[a]	44.28		3,334[a]	930[a]		122.5[x]
			73,200[a]	26	280	47.2[al]			1,059		
			62,100	19.5	266				1,022		
									720[al]		

Principal life history data are presented for each currently recognized primate species when they could be found in the literature. One should note the large number of empty cells and the variation in some variables used in the literature. All values without superscript are from Rowe and Myers (2013). Other sources are listed below

BM (body mass) = mean body mass (g) of wild adult females, ~ indicates mixed or unknown sex sample; AFR (age at first reproduction) = mean age (years) of first female reproduction; GL (gestation length) = mean gestation length (days); IBI (interbirth interval) = mean interbirth interval (month); LS (litter size) = modal litter size; NNM (neonatal mass) = mean body mass (g) of neonate females, ~ indicates mixed or unknown sex sample; WA (weaning age) = mean age at weaning (days); WM (weaning mass) = mean body mass (g) at weaning; L (longevity) = maximal recorded life span in years. Parameters are expressed as ranges if single mean values are not provided in the cited literature, LR = low range (= minimum), HR = high range (= maximum)

[a]Kappeler and Pereira (2003); [b]Groeneveld et al. (2011); [c]Kamilar et al. (2010); [d]Catlett et al. (2010); [e]Harvey et al. (1987); [f]Hakeem et al. (1996); [g]Barrickman and Lin (2010); [h]Rasoloarison et al. (2000); [i]Génin (2008); [j]Wrogemann et al. (2001); [k]Zimmermann and Radespiel (unpublished data); [l]Radespiel and Zimmermann (unpublished data); [m]Schmelting et al. (2000); [n]Cummings et al. (2012); [o]Barrickman et al. (2008); [p]Louis et al. (2006a); [q]Ross and Jones (1999); [r]Martin (2007); [s]Ross (1988); [t]Louis et al. (2006b); [u]Zimmermann and Randrianambinina (unpublished data); [v]Randrianambinina et al. (2007); [w]Volampeno et al. (2011); [x]Mumby and Vinicius (2008); [y]Tecot (2010); [z]Mutschler et al. (2000); [aa]Andriantompohavana et al. (2007); [ab]Guthrie and Frost (2011); [ac]Ramanankirahina et al. (2011); [ad]King et al. (2011); [ae]Pollock (1975); [af]Zimmermann (1989); [ag]Nash et al. (2013); [ah]Kingdon (1997); [ai]Bearder (1987); [aj]Atramentowicz (1996); [ak]Huck et al. (2011); [al]Bromage et al. (2012); [am]Lee et al. (1991); [an]Hogg and Walker (2011); [ao]Wirz and Riviello (2008); [ap]Mustoe et al. (2012); [aq]Chapman et al. (1990); [ar]Soini (1982); [as]Robinson et al. (1987); [at]Arroyo-Rodríguez et al. (2008); [au]Cords (1987); [av]Borries et al. (2011); [aw]Fürtbauer et al. (2010); [ax]Okamoto et al. (2000); [ay]Lee (1999); [az]Rao et al. (1998); [ba]Jin et al. (2009); [bb]Solanki et al. (2007); [bc]Ross and MacLarnon (2000); [bd]Zhao et al. (2008); [be]Rudran (1973); [bf]Erb et al. (2012); [bg]Tilson (1981); [bh]Reichard and Barelli (2008); [bi]Alvarez (2000); [bj]Wich et al. (2004); [bk]Langergraber et al. (2012); [bl]Kano (1992)

Cross-References

- ▶ Cooperation, Coalition, Alliances
- ▶ Estimation of Basic Life History Data of Fossil Hominoids
- ▶ Evolution of the Primate Brain
- ▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
- ▶ General Principles of Evolutionary Morphology
- ▶ Great Ape Social Systems
- ▶ Origin of Modern Humans
- ▶ Primate Intelligence
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology
- ▶ Theory of Mind: A Primatological Perspective

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Great Ape Social Systems

Angela Meder

Contents

Abstract

For decades, the social systems of the great ape species were described as being fundamentally different, but long-term field studies have questioned this idea. Although orangutans seem to be less social than the African apes, they have the ability to socialize and spend much time in contact with conspecifics if ecological conditions permit. Although the social behavior of chimpanzees and bonobos seems very different, their social structure is similar. The social systems of all great apes have common traits. They are characterized by weak ties, female transfer is common, they have a tendency toward fission-fusion grouping and a complex social network, females lack sharply defined dominance relations, and intrasexual bonds among non-kin can be relatively strong. There is remarkable

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A. Meder (✉)
Berggorilla und Regenwald Direkthilfe, Stuttgart, Germany
e-mail: kontakt@angela-meder.de; angela.meder@t-online.de

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intraspecific variability in social organization and structure; differences in ecological conditions seem to be very important in determining this. Frugivory especially requires a mobile and flexible social system. Compared to the great apes, humans show even greater variability.

Introduction

Great apes share a common ancestor, they live in similar habitats (at least some populations), they are rather large, and they have slow life histories. Despite these similarities, they developed different social structures. What are the similarities? What are the differences and why did they develop? What social structure might the common ancestor have had? What does this mean for *Homo*, which emerged from within the great apes?

These questions have occupied primatologists for decades. Many hypotheses and models were developed and had to be abandoned because the growing evidence from field research did not support them. Some questions cannot be answered satisfactorily yet, but researchers have a much better idea now of the social systems of man's closest relatives. This knowledge is summarized here. Ecology and life history are also briefly portrayed for each species because they are key factors for the understanding of group structures and dynamics.

Primate Social Systems

Animals may live in groups to increase their survival and reproductive success, but these groups have different structures for each species. To explain social systems, Kappeler and van Schaik (2002) distinguish three components: social organization (group size and organization), mating system, and social structure (relationships between group members). These three components are used here to clarify the social structures of the ape species.

Dunbar (1988) lists four reasons why primates should associate (stay and move) with conspecifics: better protection against predators, defense of resources, foraging efficiency, and improved caregiving opportunities. But sociality also has costs, especially higher intraspecific competition. Competition means usually competition for food (Kummer 1971; Wrangham 1979). Large groups deplete food more quickly and have to travel further in a day; this may influence female grouping patterns and restrict travel and sociality of females with infants (Sommer and Reichard 2000).

Folivores do not need to travel far each day and can live in relatively large groups without high levels of competition. The distance a group of a frugivore species has to travel is related to group size, so food distribution limits the number of group members (at least during feeding). Therefore, frugivores should either live in small groups or in fluctuating grouping patterns.

According to Dunbar (1988), several other factors may also influence primate group structure, at least theoretically. An important factor in this respect is the risk of male infanticide. Females with long lactation (like great apes) face an increased risk of infanticide, particularly when a reproductively capable male comes into a position of top dominance (van Schaik 2000). Usually male infanticide is seen, especially in one-male groups, as a strategy to increase reproductive success: the female will become receptive again sooner and the bond between the partners will be strengthened.

Regarding reproductive systems, the ape species have traditionally been classified as follows (Sommer and Reichard 2000):

- One male-many females (*polygyny*): gorillas
- One male-one female (*monogamy*): gibbons
- Many males-many females (*polygynandry*): chimpanzees
- Many males-one female (*polyandry*): not generally present in apes

As in this list, certain social systems have often been attributed to certain mating systems, but this is much too simple, not only in apes but also in primates in general. A social unit has its own history; a group may be polygynous or polyandrous, for example, and temporarily this may mean monogamy, but one individual may have several successive partners during its lifetime. Moreover, primates, and especially the great apes, show considerable flexibility and variability in their social behavior.

Finally, grouping levels may form a hierarchy. In great apes, the fission-fusion society is such a multilevel social system. Fission-fusion means that groups with different size and different composition may form for limited periods of time but that above this lowest grouping level, there is a higher, stable social unit. According to Lehmann et al. (2007) the advantage of fission-fusion societies is that the community size can increase.

The “Lesser” Apes

Although this chapter concentrates on the family Hominidae [used here to include great apes as well as humans], the sister family Hylobatidae will be briefly discussed. Gibbons are much smaller than the great apes: they weigh about 5–11 kg, with the siamang being the largest species. They live mostly in evergreen rain forest, with some populations in semideciduous and mixed evergreen forest. They are strictly arboreal and are primarily frugivorous.

For a long time gibbons were regarded as one of the few monogamous primate taxa, but this concept has been questioned. Change or replacement of a partner occurs in many species; in Khao Yai (Thailand), where the population density is very high, there is intense competition for females. The majority of adults copulate or attempt to copulate with partners other than their mates. Social polyandry is not uncommon, and male immigration into existing monogamous groups is observed.

Extensive overlap of territories and a wide range of affiliative interactions with neighbors have been described in several gibbon species (Sommer and Reichard 2000). They show a high interspecies variation in social structure, but even if Brockelman et al. (1998) question it, their basic social structure seems to be the nuclear family unit.

Traditionally, the male-female relationship was regarded as pair-bonded, but it seems that gibbons rather live in small groups, most probably because selective pressures do not permit large groups. At least in some species, these social units are not really two-adult groups, although it is the norm. There is a remarkable intraspecific flexibility in social organization and affiliation (Reichard and Barelli 2008). Sommer and Reichard (2000) suggest that male gibbons associate with females in order to provide a constraint to roving males and thus protect their offspring from infanticide.

The Great Apes

The species of great apes, and their distributions, are summarized in the table below:

Orangutans (Genus *Pongo*)

Bornean and Sumatran orangutans are today usually classed as two distinct species (Table 1). There seem to be characteristic differences between the two species in behavior and social organization.

Ecology

Orangutans live in rainforest habitats with a high tree species diversity from sea-level swamp forests to mountain slopes (Galdikas 1988; Knott 1999). They prefer the lowland forest up to about 1,000 m, usually close to streams and rivers as well as swamps. Galdikas (1988) lists 317 food types for Tanjung Puting. The orangutan diet consists of 61 % fruit; figs are their staple food. They eat meat (small mammals) on rare occasions (Rijksen and Meijaard 1999). Part of their habitat is characterized by extreme fluctuations in the type and quantity of fruit available, and this results in dramatic differences in nutritional intake and body weight (Knott 1999).

Orangutans require a large area that typically includes varied habitats. Resident females have stable, overlapping home ranges with an area of 0.5–6 km^2 in Borneo and 1–3 km^2 in Sumatra. The ranges are not actively defended and overlap considerably. The size of a resident adult male's home range is 1–8 km^2 on Borneo and 6–10 km^2 on Sumatra. It is neither exclusive nor stable (van Schaik and van Hooff 1996; Rijksen and Meijaard 1999; Singleton and van Schaik 2002; Stoinski et al. 2009). Daily travel distances vary from 90 m to 3.1 km (mean: 0.79 km) in Tanjung Puting.

Table 1 Great ape species and subspecies and their distribution

Species/subspecies	Distribution	Study sites mentioned here	Habitat
Pongo abelii Sumatran orangutan	Sumatra	Gunung Leuser (Ketambe, Suaq Balimbing)	Rain forest, swamp forest
Pongo pygmaeus Bornean orangutan			
Pongo pygmaeus pygmaeus Northwest Bornean orangutan	Sarawak, northwest Kalimantan		Rain forest, swamp forest
Pongo pygmaeus wurmbii Central Bornean orangutan	Southern west Kalimantan, central Kalimantan	Tanjung Puting	Rain forest, swamp forest
Pongo pygmaeus morio Northeast Bornean orangutan	East Kalimantan, Sabah	Kutai	Rain forest, swamp forest
Gorilla beringei-eastern gorilla			
Gorilla beringei beringei mountain gorilla	Virunga Volcanoes, Bwindi (Uganda)	Virunga Volcanoes, Bwindi	Montane forest, occasionally grassland
Gorilla beringei graueri eastern lowland gorilla, Grauer's gorilla	Eastern D. R. Congo	Kahuzi-Biega (mountains), Utu, Masisi (extinct)	Lowland rain forest, montane forest, occasionally swamps
Gorilla gorilla-western gorilla			
Gorilla gorilla diehli Cross River gorilla	Cross River area (Nigeria/Cameroon)	Cross River National Park, Afi, Takamanda	Lowland rain forest, montane forest
Gorilla gorilla gorilla Western lowland gorilla	From Cameroon to Cabinda and D. R. Congo in the west to the Central African Republic and the Congo Republic in the east	Lopé, Nouabalé-Ndoki (Mbeli Bai), Dzanga-Sangha (Bai Hokou), Lossi, Odzala, Río Muni, Lokoué Bai	Lowland rain forest, occasionally grassland and swamps
Pan troglodytes-chimpanzee			
Pan troglodytes schweinfurthii Eastern chimpanzee	D. R. Congo, north of the Congo River from its junction with the Oubangui into South Sudan and the Ituri region to the Rutshuru district, Uganda, Rwanda, Burundi, Tanzania	Gombe, Mahale, Bwindi, Budongo, Kibale, Semliki, Kahuzi-Biega	Rain forest, woodland, gallery forest, semideciduous forest, lowland and montane rain forest

(*continued*)

Table 1 (continued)

Species/subspecies	Distribution	Study sites mentioned here	Habitat
Pan troglodytes troglodytes Central chimpanzee	From the Congo River mouth to the Congo Republic and the Central African Republic to Cameroon, north to the Sanaga River	Lossi, Lopé, Río Muni, Ndoki	Rain forest
Pan troglodytes ellioti East Nigeria-West Cameroon chimpanzee	Nigeria and Cameroon to the Sanaga River	Gashaka	Lowland forest, montane forest, woodland
Pan troglodytes verus West African chimpanzee	West Africa to Togo in the east	Taï, Assirik, Bossou	Savanna, deciduous forest, rain forest
Pan paniscus Bonobo	D. R. Congo, south of the Congo River	Lomako, Wamba, Lukuru	Rain forest, swamp forest, occasionally grassland, dry forest

Taxonomy according to IUCN 2012

Orangutans are the largest arboreal animals. Females move almost exclusively at between 10- and 25-m height in the trees. In Tanjung Puting, males sometimes walk on the ground, where they also forage and rest, but not in Sumatra, where tigers occur (Sugardjito et al. 1987; Galdikas 1988).

Life Histories and Dispersal

Orangutans may be nursed until 6 years old, longer than any other ape species. The mean interbirth interval in Sumatra is 8–9 years and in Borneo 6–7.7 years (Wich et al. 2009). Females may conceive from about 11 years (Knott 1999). Fully adult (flanged) Bornean males weigh 86.2 kg on average and females 38.7 kg; a single Sumatran male weighed 86.2 kg and Sumatran females on average 38.3 kg (Markham and Groves 1990). Apparently mature but unflanged males weigh about 60–70 kg. In captivity, orangutans have reached as much as 58 years of age, whereas in the wild their maximum age is estimated at 45 years (Leighton et al. 1995).

On reaching adulthood, males develop typical secondary sexual characteristics: flanged cheeks and a big throat sac which enables them to produce loud calls ("flanged" males). Some males show an extended subadult appearance ("unflanged" males) in some cases until the age of 30. This parallel existence of two morphs of mature males is called bimaturism (Utami Atmoko and van Hooff 2004). Orangutan male bimaturism is socially influenced; the close presence of a flanged male suppresses the development of secondary sexual characteristics in subordinate males (van Hooff 1995).

Females often stay in ranges that overlap or are close to their natal area (Galdikas 1984; Singleton and van Schaik 2002). Despite these observations, Utami et al. (2002) found that adult males and females are mostly unrelated in Sumatra – this means that both sexes disperse. Males generally seem to disperse more widely (van Schaik and van Hooff 1996; Morrogh-Bernard et al. 2011; van Noordwijk et al. 2012).

Regarding their ranging behavior, Rijksen and Meijaard (1999) discern three types of orangutans: residents, who stay in the same area for years; commuters, who appear regularly and have a very large home range; and wanderers, who are seen very infrequently and seem to have no home range at all. There are considerable between-site differences in the percentage of these types. In some sites in Sumatra, no residents are found at all. In Ketambe, commuters are the majority of the population (Rijksen and Meijaard 1999; van Schaik 1999).

Size and Structure of Associations

In both species of orangutans, the individuals move independently most of the time. Usually, trees do not provide enough food for several adults. It is difficult to get statistical data on the sizes of associations, because all field studies bias toward larger party sizes, since they are found more easily. The mean daily party size is 1.67 independent individuals in Suaq Balimbing, and the largest sustained party size that has been observed so far was 10.67 (van Schaik 1999).

It is sometimes difficult to decide whether orangutan associations can be called social or whether the apes just meet during their search for food and tolerate the presence of each other. According to Galdikas (1984), in Kutai only 6 out of 13 groups could be considered “social”: a consorting adult pair and two female-offspring units. In Tanjung Puting, Galdikas (1995) observed that 94 % of the time adolescent females who are in contact with others included true social interaction; the rest is nonsocial aggregation. In other age/sex classes, roughly 80–90 % of associations are true social groupings.

The most common grouping is one subadult male and one unreceptive adolescent female (Galdikas 1988). Subadult males and adolescent females spend about 40 % of their time in contact with other units in Tanjung Puting, adult males 16.8 %, and adult females 13.5 % (Galdikas 1995). Adult females in Borneo are far more solitary than those in Sumatra; this reflects the difference in average orangutan density (van Schaik 1999). Fully adult males suffer energetically from association and thus are extremely solitary (van Schaik and van Hooff 1996; Knott 2009). The largest stable parties in Suaq Balimbing develop when females converge upon a dominant male. Sexual associations seem to last longer there and involve more animals than elsewhere (van Schaik 1999).

Male-Female Relationships and Mating Strategies

Contacts of adolescent females with adult males in Tanjung Puting are almost totally restricted to consortships which the female initiates, maintains, and terminates. In general, adult females either avoid contact with males or ignore them, while adolescent females (9–14 years) spend 56 % of their contact time exclusively with males. Toward adult males, nonreceptive adolescent and adult females show avoidance or indifference; if they are receptive, however, they are highly motivated to maintain contact with the seemingly indifferent adult males and may respond to their long calls by immediate approach. With subadult males, adolescent females have long-term associations with no copulation, which may be called friendships, as well as short associations, but no consortships (Wich et al. 2006). The subadult males are responsible for maintaining contact with nonreceptive adolescent females, and sometimes they travel with them for weeks (Galdikas 1984, 1995).

There are two behavioral tactics in the mating strategy of male orangutans: resident flanged males sit, utter long calls, and wait for females (residents, commuters, and wanderers), while unflanged and nonresident flanged males actively search for females and mate with them, irrespective of their receptivity (Utami Atmoko and van Hooff 2004; Stumpf et al. 2008; Knott 2009). Rijksen and Meijaard (1999) assume that these “rapes” are a sexual strategy of young males because the ascent to a higher social status is associated with long-lasting sexual relationships with several females, and this status may be the prerequisite for the development of the full sexual characteristics (Utami et al. 2002). During consortship, the partners travel closely for days or even weeks, usually with the adult male following (Galdikas 1984; Singleton and van Schaik 2002). Severe mating competition is usual among fully adult orangutan males, but no infanticide attempts have ever been seen so far.

Both mating tactics are successful. A paternity analysis in Ketambe, Sumatra, showed that all but one of 11 infants were sired by resident males; out of these ten infants, six were sired by unflanged males (Utami et al. 2002). There is more variation in orangutan mating patterns than previously thought (Utami Atmoko et al. 2009a). In general, however, unflanged males seem to have a slightly lower reproductive success (Satkoski et al. 2004).

Female-Female Relationships

Competition for access to limited resources is rare. In Sumatra, where the population density is high, female home ranges overlap considerably and the rates of association between females are high compared to Borneo (Singleton and van Schaik 2002; Knott et al. 2008). The longest association Galdikas (1984) observed between two adult females in Tanjung Puting was 3 days and 2 nights. Sometimes females travel together, but few direct interactions are observed. Their behavior toward each other varies from aggression and avoidance to affiliative activities, but only very rarely does a female touch another female affiliatively.

Adolescent females often travel together after encounters. The longest association Galdikas (1995) saw lasted at least 10 days. Although adult females are often intolerant to and may attack adolescent females, the adolescents try to associate with them.

Male-Male Relationships

Flanged males avoid each other. They produce long calls that carry for up to 1 km, especially when they approach another individual, after they have defeated another adult male or before they travel over long distances. When adult males come close to each other, agonistic interactions are observed. They have the highest incidence of disfigurements among orangutans, presumably from injurious fights. They dominate unflanged males but may tolerate them as long as they keep a certain distance (van Schaik and van Hooff 1996; Utami Atmoko et al. 2009b).

Discussion: Genus *Pongo*

An older model of orangutan social relationships is that a fully adult male controls a relatively large range that includes the smaller ranges of several females. Calculations proved, however, that a male can maximally defend 0.37–0.57 km^2, which is less than the size of a single female's range. Moreover, adult male ranges overlap and mating is promiscuous (van Schaik and van Hooff 1996).

Orangutans have been regarded as solitary, but they have the ability to socialize and spend much time in contact with conspecifics if ecological conditions permit. That they are not antisocial is documented from zoos, where they have been kept in rather large groups (Poole 1987). Restrictions on group size must therefore lie in the environment in the wild (Harrison and Chivers 2007).

To associate with conspecifics in feeding parties is costly if the food in one tree is not sufficient for several adults (especially for large males). But social contacts are important, particularly for the development of various behaviors and of social competence and relationships. Females with new offspring therefore form "nursery groups" in which new and weaned offspring can socialize (Galdikas 1995; van Schaik 1999; van Noordwijk et al. 2012). Infants learn there how to behave correctly toward conspecifics. Even in independent immature animals, social contact is still necessary for further development. According to Galdikas (1995), adolescent females use social contacts to establish their own home range and to form relationships with the individuals in adjacent ranges. Sugardjito et al. (1987) discuss more benefits of grouping.

Orangutans show the greatest degree of sexual dimorphism of all great apes. Such an extreme dimorphism may be a result of female choice or male-male competition. Other species with such sexual dimorphism are usually either living in one-male groups or have a lek-type mating system. Rijksen and Meijaard (1999) suggest that orangutans have a very complex lek-type mating system. Males meet in a "social arena," an area with especially abundant food resources, where the ranges of several residents overlap and where commuters and wanderers visit regularly. In that arena they emit long calls to attract females.

Two models for the description of the orangutan social system are discussed by van Schaik and van Hooff (1996): either a roving male promiscuity system (an estrous female attracts multiple males who compete vehemently for sexual access to her) with no higher-level social unit or a spatially dispersed but socially distinct community organized around one or more large adult males. Both models have weaknesses: well-defined communities do not seem to exist in any orang population and orangutan females do not mate with any available male. They seem to show distinct preferences; individual relationships and bonding are important

(Galdikas 1984; van Schaik and van Hooff 1996; Rijksen and Meijaard 1999; van Schaik 1999; Utami et al. 2002; Stumpf et al. 2008; Utami Atmoko et al. 2009a). The roving male promiscuity system seems to be closer to the situation of the Bornean orangutans, and the socially distinct community system organized around a dominant male fits better for the Sumatran population (Singleton and van Schaik 2002; Mitra Setia et al. 2009).

Although orangutan communities comparable to those of chimpanzees do not exist, orangutans obviously have a social network. Residents and commuters in a certain area seem to know each other well, while wanderers are strangers to them. An explanation could be provided by a suggestion by Rijksen and Meijaard (1999) and van Schaik (1999) that the individual-based fission-fusion social system that is characteristic for chimpanzees may also be typical for orangutan societies; the differences are in degree rather than in quality.

Gorillas (Genus *Gorilla*)

Eastern and western gorillas are today usually classed as two distinct species (Table 1). Long-term studies are available now for both species from several sites.

Ecology

Gorillas live in a variety of habitats: lowland rain forest, swamp forest, marshy clearings (bais), and montane forest. The lowest densities of western lowland gorillas are observed in areas without Marantaceae and Zingiberaceae, their preferred food are plants, and the highest densities in Marantaceae and swamp forest (Poulsen and Clark 2004; Rogers et al. 2004).

Mountain gorillas mainly feed on green plant parts, whereas lowland gorillas eat a lot of fruit (but still markedly less than chimpanzees and orangutans). Utilization of fruit and of herbaceous vegetation varies seasonally. Western lowland gorillas eat about 250 food items with up to about 100 fruit species, while the mountain gorillas of the Virunga Volcanoes eat only up to 72 different plant species and very few fruits (Tutin and Fernandez 1993; McNeilage 2001; Doran et al. 2002a). Gorillas do not kill vertebrates but eat small animals, mainly insects.

Gorillas do not occupy territories. Their annual home range covers about 8 km^2 in the Virunga gorillas, about 30–40 km^2 in Grauer's gorillas, and 11–30 km^2 in western lowland gorillas. The size depends on the distribution of food sources and group size; home ranges overlap (Tutin 1996; Remis 1997; McNeilage 2001; Yamagiwa et al. 2003a, 2012; Bermejo 2004). In general, gorilla groups move an average of 0.5–2 km a day to forage. Folivorous gorilla populations in montane forest show a shorter daily journey length than more frugivorous populations (Yamagiwa et al. 2003a, b; Robbins et al. 2006).

Apart from humans, gorillas do not really have "predators." The only predator is the leopard (Tutin and Fernandez 1991; Fay et al. 1995). They live primarily on the ground, particularly in the Virunga Volcanoes, where females spend only 7 % of the time above the ground and males 2 % (Doran and McNeilage 1998). Silverback males do not often leave the ground because of their great weight. Gorillas sleep on bare earth or in nests, which they build on the ground or in trees (Poulsen and Clark 2004).

Life Histories and Dispersal

Gorilla infants are nursed for at least 2–3 years in Virunga gorillas, which develop faster than other populations, and for 4 years in western lowland gorillas; the interbirth interval is about 4–5 years (Breuer et al. 2009). Gorillas grow faster and breed more rapidly than other hominids (Groves and Meder 2001). Females may first reproduce between about 8 and 9 years of age in the wild (Watts 1991; Robbins et al. 2004). Males are fully grown at approximately 15 years of age and are called silverbacks. Young mature males without the secondary sexual characteristics are called blackbacks. Western lowland gorilla males have a mean weight of 149 kg and females 71.5 kg, mountain gorilla males weigh 157 kg and females 97.7 kg, and Grauer's gorilla males 171 kg and females 80 kg (Meder 1993; Rowe 1996). Adults have a relatively short life expectancy; silverback males, in particular, seem to have a hard life and die young (Groves and Meder 2001). In the wild, they probably reach 40–45 years; in captivity, several individuals have lived more than 50 years.

Reaching adulthood, female gorillas usually leave the group they were born in and join a new unit. They emigrate only if they encounter another male and may transfer several times before they settle down in a certain group (Watts 1996; Sicotte 2001; Stokes et al. 2003). In Kahuzi-Biega, the simultaneous transfer of several individuals was observed (Yamagiwa and Kahekwa 2001; Yamagiwa et al. 2009).

In western gorillas and Grauer's gorillas, male emigration is common, while among mountain gorillas less than 50 % of the males emigrate (Stoinski et al. 2009a). If they leave, they either become solitary or join all-male groups in some populations (Watts 2000; Yamagiwa et al. 2003a; Robbins et al. 2004). In western lowland gorillas (Lokoué Bai, Congo), even subadults and juveniles may emigrate (Gatti et al. 2004). Solitary males may travel very long distances (Douadi et al. 2007).

Size and Structure of Social Units

In a gorilla group there is a clear hierarchy. The leading silverback has the highest rank, and adult females are dominant over young animals. In most populations, groups usually consist of one adult male, several females, and their offspring (Magliocca et al. 1999; Yamagiwa et al. 2003a; Gatti et al. 2004). In the Virunga mountains, in Bwindi and Bai Hokou, however, a large percentage of the groups include more than one adult male (Table 2; Goldsmith 2003; Kalpers et al. 2003; Yamagiwa et al. 2012).

As groups contain more females than males, many males are "left over." Gatti et al. (2004) found that at Lokoué Bai, 42 % of the silverbacks are unmated: 31 % are solitary and 11 % live in nonbreeding groups. Solitary males make up 5–10 % of

Table 2 Gorilla group sizes (including unweaned immatures)

Region	Group size		Sample size	Number of silverbacks	Source
	Mean	Range		Mean	
Gorilla gorilla gorilla					
Mt. Alen, Río Muni	7.13	2–12	8		Jones and Sabater Pí (1971)
Abumnzok-Añinzok, Río Muni	6.4	3–19	5		Jones and Sabater Pí (1971)
Ndoki, Congo	7.3	5–12	7		Mitani et al. (1993)
Lokoué Bai, Congo	7.7	2–15	45		Gatti et al. (2004)
Mbeli Bai, Congo	8.4	2–16	14	1.1	Parnell (2002)
Maya Nord, Odzala, Congo	11.2	2–22	31	1.0	Magliocca et al. (1999)
Lossi, Congo	17	7–32	8		Bermejo (1999)
Lopé, Gabon	9.3	4–15	4	1.25	Tutin et al. (1992)
Gorilla beringei graueri					
Kahuzi-Biega, mountains	14.3	3–42	12	1.2	Yamagiwa (1983)
	15.6	6–37	14	1.1	Murnyak (1981)
	10.0	2–24	25		Yamagiwa et al. (1993)
Kahuzi-Biega, lowland (Utu)	15	4–25	6		Cordier (Schaller 1963)
Masisi	8	3–11	3		Yamagiwa et al. (1989)
Gorilla beringei beringei					
Virunga Volcanoes	16.9 8.8	5–27 3–21	10 28	1.7 1.4	Schaller (1963), Weber and Vedder (1983)
	10.9	3–47	32	1.9	Kalpers et al. (2003)
	12.5	2–47	36		Gray et al. (2010)
Bwindi, Uganda	9.9	2–23	28	1.9	McNeilage et al. (2001)
	8.8	5–14	12	1.75	Harcourt (1981)
	10.7	2–27	36		Robbins et al. (2011)

the western lowland gorilla populations. Among eastern gorillas, the percentage seems to be lower: up to 3.5 % in Kahuzi-Biega and 1.8–4.0 % in mountain gorillas.

Gorillas occasionally form all-male groups, usually with one mature male and a few younger males. Such nonreproductive groups have a similar size to breeding groups; they have been observed in western lowland as well as mountain gorillas, although not in Grauer's gorillas (Robbins et al. 2004; Levréro et al. 2006). These groups as units may be long-lasting, but their membership changes quite often due to male migrations. They seem to be transition units in both gorilla species (Gatti et al. 2004; Levréro et al. 2006).

Gorilla groups can have very different histories (Robbins 2001). When the dominant male dies, the group may disperse if no subordinate silverback is there to take over the leadership; if there are two younger silverbacks, the group may split. Parnell (2002) lists five stages in the development of a typical western lowland gorilla group: nascent (one silverback + one female without offspring), infant (one silverback + one or more females with dependent offspring), juvenile (one silverback + one or more females with a range of offspring), mature (one silverback + one or more females and a range of offspring from infants to young silverbacks), and senescent (one old silverback, few or no females, only older offspring). Group takeovers by outside males have not been reported so far (Robbins et al. 2004), but in zoos new males have been introduced successfully to established groups in many cases.

The size of gorilla groups is very variable but similar among the subspecies (Table 2). An average group contains about nine to ten members (Parnell 2002; Yamagiwa et al. 2003a). Possibly groups can grow especially large where the density of their staple food is very high (Robbins et al. 2006). The largest group observed so far was Pablo's group in Rwanda with 65 members.

Male-Female Relationships and Mating Strategies

In the social system of gorillas, the high cohesiveness of a group is usually attributed to the attractiveness of the leading male to females (Yamagiwa et al. 2003a, but see Stokes 2004). Adult male-adult female relationships are considered to be the "core" of the social group; they vary depending on kinship, length of tenure, and reproductive status. Male aggression to females is common and often can be regarded as "courtship aggression." It is higher if the female is in estrus; females usually respond submissively (Robbins 2003; Bradley et al. 2005).

Wrangham (1979) suggests that a gorilla group represents a "permanent consortship." Adult females usually prefer to mate with the leading male and subadult females with subordinate males (Robbins 1999; Bradley et al. 2005; Stoinski et al. 2009b). Females in multimale groups often copulate with more than one male, despite interference by dominants (Sicotte 2001); this may confuse paternity and induce all the males to protect the infants against infanticide.

If a mountain gorilla mother transfers between groups while she has a baby, if a dominant male dies, or if another silverback male takes over the group, the baby is frequently killed by the new male (Fossey 1984; Watts 1989). Infanticide causes 37 % of infant deaths in the gorillas of the Virunga Volcanoes in one-male groups (Bradley et al. 2005; Robbins et al. 2007). Recently, evidence for infanticides was reported for Kahuzi-Biega too; possibly it had been suppressed earlier because the males of neighboring groups were related (Yamagiwa and Kahekwa 2004). Infanticide is suspected also in several cases in western lowland gorillas, when infants disappeared (Yamagiwa et al. 2009).

Female-Female Relationships

Dominance relations between females are weak, their rank depending on factors such as how long they have been in the group (Watts 2001; Kapsalis 2004). Females in large groups sometimes harass new immigrants, and aggression between females is not unusual (Watts 1996).

As females usually leave their natal group to join another group, it was long assumed that all females in gorilla groups are unrelated. In mountain gorillas, however, more than 70 % of the females spend at least some of their reproductive careers with female relatives. In western lowland gorillas, Bradley et al. (2007) found that 40 % of the adult females had an adult female relative in the same group. Female maternal relatives are close associates, often interacting affinitively and supporting each other (Watts 1996, 2000, 2001).

Male-Male relationships

As between females, there are few affiliative interactions among adult males. Severe contact aggression between males within a group is not usual (Sicotte 1994; Stoinski et al. 2009a).

Patrilineal kinship is important for mountain gorilla males because they often remain in their natal group instead of dispersing. There they assist their fathers in resisting threats or incursions from extragroup males (Robbins 1995). Mature followers and older adolescents cooperate with dominant males against extragroup males (Watts 2000). Dominant males try to prevent these followers, however, from mating with females other than the dominants' daughters. Coalitions of brothers may occur but are probably uncommon (Watts 1996).

Intergroup Interactions

The home ranges of various gorilla groups and of lone silverback males overlap, so encounters are frequent, but the leaders of breeding groups generally avoid them. In mountain gorillas on average, about one encounter per month is observed; it often includes aggression between silverback males. They try to drive competitors away by displaying or attacking (Yamagiwa 1987; Watts 1991; Robbins 2003). During such encounters, extragroup matings have been observed (Sicotte 2001).

Western lowland gorilla males generally show less contact aggression during encounters than mountain gorillas. They often meet in swamps or fruiting trees; the groups may feed together without hostility (Tutin 1996; Magliocca and

Gautier-Hion 2004). They occasionally intermingle peacefully and even may nest together for one night (Kuroda et al. 1996; Doran and McNeilage 1998; Bermejo 2004). In Lossi, silverbacks often react aggressively to lone males, but usually they tolerate other groups – their reaction varies, however, and depends on the identity of the silverback (Bermejo 2004).

Discussion: Genus *Gorilla*

Differences in ecological conditions seem to be more important in determining the social system of a gorilla population than its taxonomy. Mean group sizes seem to be similar across the genus *Gorilla* (Table 2), but in populations with a highly folivorous diet, the groups may become larger (Goldsmith 2003).

There seems to be a considerable influence of fruit availability on ranging and grouping patterns. During the fruiting season, large groups travel farther than small groups in western lowland gorillas as well as Bwindi gorillas. To reduce competition, the groups may spread more widely during feeding and/or form temporary foraging subgroups in western lowland gorillas and Grauer’s gorillas (Tutin 1996; Remis 1997; Parnell 2002; Goldsmith 2003; Yamagiwa et al. 2003a), which may feed and even nest more than 1 km away from the rest of the group (Bermejo 2004).

Parnell (2002) assumes that a high proportion of multimale groups in some populations may have developed because solitary males face unusually high odds against establishing a group and the current demographic conditions deter maturing males from emigration. As multimale groups provide better protection from infanticide, females may prefer groups with more than one male in the future (Watts 1996, 2000; Yamagiwa et al. 2003a; Yamagiwa and Kahekwa 2004). Dominant males may tolerate the presence of mating activities of younger males to reduce the risk of later infanticide (Robbins 1995).

Maryanski (1987) introduced the hypothesis that gorillas, like chimpanzees, live in an “open-group system”: several gorilla groups and lone males share a home range where they meet preferred groups, socialize, and then depart. There is no evidence that a higher unit like the chimpanzee community exists in gorillas, but in some gorilla populations, there do seem to be strong ties between different groups. Yamagiwa and Kahekwa (2004) observed group fission in Kahuzi-Biega, which resulted in several neighboring groups with related males.

It seems that two types of association among related males evolved in gorillas: association within a group and tolerance between males of neighboring groups. The occurrence of infanticide may promote the former, and its absence may promote the latter. The social structure of gorillas may be very flexible and allow them to choose either type of social organization, even in the same population (Yamagiwa and Kahekwa 2004).

Chimpanzees (Genus *Pan*)

Although the two species of the genus *Pan* (the “common” or robust chimpanzee and the “pygmy” or gracile chimpanzee, or bonobo) share many characteristics – physical as well as social – there are marked differences. These presumably result from their separation by the Congo River. One of the common characters distinguishing them from the other apes is a low degree of sexual dimorphism in body size, but instead a large swelling of the anogenital region in females and large testicles and penises in males.

Chimpanzee (*Pan troglodytes*)

Ecology

Chimpanzees have been studied at a number of sites (Table 1). They live in a wide variety of habitats in tropical Africa, from rain forest to closed and open forest, gallery forest, open savanna and grassland, as well as montane rain forest up to 2,400 m. In Ndoki, Poulsen and Clark (2004) found the highest density in swamp forest.

Chimpanzees are mainly frugivorous. Their diet consists of 48–82 % fruit, the rest consisting of leaves and other plant parts, and also more animals than other great apes, including insects as well as vertebrates, which are hunted communally (Goodall 1986; Chapman et al. 1994). The number of plant food items ranges from 55 to 328, depending on the habitat. Their diet varies seasonally, and this results in seasonal body weight fluctuations (Nishida 1990; Tutin and Fernandez 1993; Basabose 2002).

The home ranges (or territories) of chimpanzee communities vary according to habitat, season, community size, and the risk of encountering neighboring communities. The mean size is 21.6 km^2. In open landscapes, where food is dispersed widely, the density is very low and the home range extraordinarily large, up to 560 km^2. Home ranges of neighboring communities overlap (Yamagiwa 1999; Boesch and Boesch-Achermann 2000).

Within the community's home range, each adult has his/her own core area. Most females show strong fidelity to an area once they settle there as an adult (Williams et al. 2002b, 2004). Males have larger home ranges than females (Hasegawa 1990; Chapman and Wrangham 1993; Lehmann and Boesch 2005). The mean daily travel distance of individuals is about 3 km (Doran 1997; Boesch and Boesch-Achermann 2000).

In Taï, leopards attack chimpanzee; at other sites, lions prey on them (Tsukahara 1993; Boesch and Boesch-Achermann 2000). About 50 % of the day chimpanzees stay above ground level. They spend the night in nests that are usually built in trees up to 50-m high (Poulsen and Clark 2004), although terrestrial nesting has also been observed in some areas, for example, in Guinea (Koops et al. 2004).

Life Histories and Dispersal

Chimpanzee infants are nursed for about 3–4 years. The interbirth interval is usually 4–7 years (Nishida et al. 1990; Boesch and Boesch-Achermann 2000). Females may first conceive at about 9–11 years.

The mean weight of adult male *Pan troglodytes troglodytes* is 53 kg, of females 43.8 kg; *Pan troglodytes schweinfurthii* males weigh 40.5 kg and females 32.9 kg (Groves 2001), but even within each subspecies, there is great variation both within and between populations.

The maximal age of wild chimpanzees is not yet very well known. Boesch and Boesch-Achermann (2000) assume that they may reach 50 years. In captivity, they have lived for almost 60 years.

In most populations, females usually leave their natal groups upon maturity. At Gombe, most or all adolescent females visit other communities, and some may even conceive there, but only 50 % of them emigrate permanently, the others returning to their natal communities (Pusey et al. 1997). In Taï, on the other hand, almost all females transfer (Boesch and Boesch-Achermann 2000). In Mahale, the transfer process lasts from 6 months to 2 years, while the females associate and mate with the males of the two communities, and 13 % of the females transfer more than once there (Nishida et al. 1990). Male chimpanzees do not emigrate and cannot migrate between communities (Goodall 1986). Nevertheless, captive chimpanzees can be induced to accept new males into their group (Wilson and Wrangham 2003).

Size and Structure of Social Units

Chimpanzees live in fission-fusion groups within their communities. They have two levels of social unit: the smaller association unit is the party or subgroup – temporary and very variable – and the higher-level unit is the (stable) community or unit group (Table 3). Members of a community meet occasionally (fusion) and travel for longer or shorter periods in parties until they separate again (fission). On average, a party stays constant in size and composition for 24 min in Taï, in Gombe for 69, in Bossou for 126, and in Budongo for 14 min (Boesch and Boesch-Achermann 2000).

In Gombe, the average party size is 3.5 for females only, 10.7 for mixed parties, and 4.0 for males only. Single-sex parties are significantly smaller than mixed-sex parties, and parties with more estrous females contain more males (Williams et al. 2002a). Estrous females are more gregarious than other classes, and they are especially associated with males (Goodall 1986; Pepper et al. 1999).

In several populations, nursery parties – several females with their infants – have been observed. In Gombe, females spend 65 % of their time alone or with their offspring, in Kibale even 70 %, while in Taï they are alone only 18 % of their time when fruits are abundant (Wrangham et al. 1996; Pusey et al. 1997; Lehmann and Boesch 2004). During fruit scarcity, their day range is reduced and the mean party size decreased (Doran 1997). In Mahale and Kibale, food availability and the number of estrous females are positively correlated with party size (Mitani et al. 2002), but in Budongo, Newton-Fisher et al. (2000) found no positive correlation, and Basabose (2004) found in Kahuzi-Biega that fruit abundance per se does not affect party size but seasonality and fruit distribution do.

Party size is also determined by their function. During hunts for vertebrate prey, such as monkeys in Kibale, Watts and Mitani (2002) found a significant positive

Table 3 Mean party and community size in chimpanzees (including unweaned immatures)

Population	Mean party size	Range	n	Community size	Source
Pan troglodytes schweinfurthii					
Gombe, Tanzania	5.6		498	50	Boesch (1996)
Mahale, Tanzania	6.1		218	29	Boesch (1996)
	4.0	1–24	3,818		Itoh and Nishida (2007)
Kibale, Uganda	10.3	1–47	827	140	Basabose (2004)
Budongo, Uganda	6.3	1–30	1,824	46	Newton-Fisher et al. (2000)
Kahuzi-Biega, D. R. Congo	4.43	1–13	71	22	Basabose (2004)
Pan troglodytes troglodytes					
Ndoki, Congo	7.0		32		Malenky et al. (1994)
Mt. Alen, Río Muni	4.7	2–7	3		Jones and Sabater Pí (1971)
Mt. Okoro Biko, Río Muni	11.2	4–23	5		Jones and Sabater Pí (1971)
Pan troglodytes verus					
Taï, Côte d'Ivoire	8.3	1–41	2,912	76	Boesch (1996)
Taï (during fruit scarcity)	5.75		395		Doran (1997)
Bossou, Guinea	4.0	1–9	426	20	Sakura (1994)
Assirik, Senegal	5.3		267	28	Boesch (1996)
Pan paniscus					
Lomako	4.33	1–8	87	10	White (1988)
	7.15	2–17	26	22	White (1988)
	9.69	1–18	26	21	White (1988)
	7.9	1– >50	268	>50	Badrian and Badrian (1984)
Wamba	16.9	1–54	147	58	Kuroda (1979)
	11.2				Mulavwa et al. (2008)

relationship between hunting party size and the number of kills per hunt. Success also increases with the number of males per hunting party at Gombe and Taï.

Party size depends also on community size; in large communities parties occasionally are larger than a whole small community. Therefore, Boesch and Boesch-Achermann (2000) suggest that relative mean party sizes should be compared. According to their calculation, chimpanzees have a relative mean party size of 9–21 % of the community size.

The community size may lie between 20 and 150 members. It must contain at least one adult male, but a higher number of males is usual, often more than ten.

It seems that small communities retain a fission-fusion structure, but this loses much of its flexibility and the parties remain stable for much longer periods of time than in larger communities.

Male-Female Relationships and Mating Strategies

Relationships between male and female chimpanzees are usually not very close. Grooming between them, for example, is rather infrequent compared with male-male grooming. Constant and frequent proximity is particularly found in mother-son dyads.

Chimpanzee females use a tactical strategy of mating promiscuously to confuse paternity (Stumpf et al. 2008). In Gombe, consortships have been observed in all males, and 25 % of conceptions occur during consortships (Constable et al. 2001). In Mahale, however, they are very rare and only 8.3 % of conceptions are the result of consortship (Hasegawa and Hiraiwa-Hasegawa 1990), while in Taï only one offspring was conceived during consortship; half of the males and 56 % of the females are never seen to consort.

Matsumoto-Oda (2002) reported from Mahale that females copulate more often with continuously affiliative males; therefore, males interact with anestrous females to increase the chance of mating when they are in estrus. Most authors, however, found persistent coercing male aggression for eastern chimpanzees and the females most frequently solicited the most aggressive males (Muller et al. 2011). Prime males dominate all adult females and often try to monopolize them. Estrous females are more selective in their partners (Stumpf and Boesch 2006) and most frequently stay around the alpha male in Mahale and Kibale (Takahata 1990a; Muller et al. 2011). In Gombe, the alpha male is responsible for 36–45 % of all conceptions and high-ranking males for 50 %; in Taï, 71 % of all infants are sired by high-ranking males (Constable et al. 2001; Boesch et al. 2006).

According to Williams et al. (2002b), male aggression in boundary areas forces the females to be members of their community by settling in the center of their home range. Male coercion of females is an important element, and violence toward unfamiliar females near the edges of the defended range is particularly fierce. Nevertheless, estrous females sometimes disappear for a few days and may make temporary visits to neighboring males (Boesch and Boesch-Achermann 2000). In Gombe, 13 % of copulations are with males from other communities (Goodall 1986). These extracommunity matings do not very often result in conception: in Taï, extragroup paternity was found only for 7 % of the offspring (one infant), and in Gombe, all tested offspring were sired by males of the same community (Constable et al. 2001; Vigilant et al. 2001).

Infanticide has been observed in several chimpanzee populations, especially in Mahale (Nishida et al. 1990). In Taï and Gombe, infanticide and cannibalism by females were observed (Pusey et al. 1997; Boesch and Boesch-Achermann 2000; Pusey et al. 2008). In Gombe and Mahale, more cases of infanticide were recorded within the community than between communities. These cases do not provide any evidence that infanticide is a successful male reproductive strategy in chimpanzees (Wilson and Wrangham 2003).

Female-Female Relationships

High-ranking females are the most social with other females; low-ranking females are the least. This suggests that contest competition is an important aspect of female association patterns. In Mahale and Gombe, immigrant females experience aggression from resident females (Williams et al. 2002a, b; Pusey et al. 2008).

But females may also have affiliative relationships (Lehmann and Boesch 2008; Langergraber et al. 2009). In Taï, close female associations (friendships) can last for years and are very stable; some pairs spend up to 79 % of their time together. According to Boesch and Boesch-Achermann (2000), higher intrasexual competition and higher involvement in the social interactions of males make it profitable for females in Taï to develop long-term friendships with other females and to form stable alliances.

Male-Male Relationships

Male chimpanzees associate more strongly with one another than do females with other females and males with females. They form coalitions in all populations studied (Boesch and Boesch-Achermann 2000; Newton-Fisher 2002), and apart from coalitions, friendship between males has also been observed (Nishida and Hosaka 1996). Which individuals form affiliative relationships is not clear; genetic studies in Kibale showed that maternal kinship is not strongly associated with male-male association (Kapsalis 2004).

Among the males there is a linear dominance hierarchy, and rank reversal generally results from dyadic fights (Takahata 1990b; Muller 2002). The alpha male is the most active groomer; he tends to move first and be followed by subordinates (Takahata 1990b). In Taï, the leader of a community announces his presence by drumming; this also gives information to other individuals about the direction and speed of group movement (Boesch and Boesch-Achermann 2000).

Agonistic confrontations between males are observed regularly, and they are most aggressive between the two highest-ranking males. Coalitions in attacks are frequent; in Taï it is mostly low-ranking males coalescing against dominant individuals (Boesch and Boesch-Achermann 2000). Coalitions are also formed for hunting, for the intragroup control of widely dispersed females, and to monitor territorial borders (Stanford 1998).

Intergroup Interactions

Most interactions of chimpanzee males with neighboring communities involve only auditory contact-pant-hoots, a long-distance call. These pant-hoots are also used to advertise their presence and numerical strength. Males almost always show fear or hostility to strange males (Wilson and Wrangham 2003).

Chimpanzee males invest considerable time and energy in defending the home range of their community or locating their neighbors; the home range is controlled by groups of at least four males on a weekly basis in Taï (Boesch and Boesch-Achermann 2000). During those patrols, they remain silent and actively search for signs of the neighbors. They make incursions into the home ranges of the neighbor communities, sometimes of more than 1 km, and if they encounter strange males, they attack them. In Tai, they are sometimes joined by females (Lehmann and Boesch 2005). Not only males are attacked but females too, except for tumescent females (Pusey 2001; Williams et al. 2004; Watts et al. 2006). Females with or without infants often join attacks, but they tend to avoid direct physical contact with members of the other community.

Hostile intercommunity relations have been observed at all sites. Intraspecific violence is one of the leading causes of mortality for eastern chimpanzees (Wilson et al. 2004). At Gombe and Mahale, the destruction of a small community by a larger one, including systematic attacks and killing of individuals by males from a larger community, has been observed. Wilson and Wrangham (2003) provide a good overview of such intercommunity conflicts. So far, there is no consistent evidence from the field that the communities find more or better sexual partners and new resources as a result of the fights (Boesch and Boesch-Achermann 2000, but see Mitani et al. 2010). Extensive female transfer after a violent fight between communities was observed only in Mahale (Wilson and Wrangham 2003). In Gombe, adult parous females join other communities only when all males of their community have been killed.

Williams et al. (2004) conclude that male chimpanzees cooperatively defend territories that contain food resources for themselves, their long-term female mates, and their offspring, and they try to extend the size of the community's home range because a larger area means greater availability of food and higher female reproduction. Infanticide during intercommunity encounters can also be interpreted as the removal of future competitors. Concerning intercommunity killings by adult males, data from various study sites most strongly support the hypothesis that attackers reduce the future coalition strength of rival communities.

Bonobo (*Pan paniscus*)

The most important sites where bonobos have been studied are listed in Table 1.

Ecology

The typical habitat for bonobos is the lowland rain forests and swamp forests of the Congo Basin. In some areas, they also live in dry forest and visit grassland. They eat up to 147 food items; 72–90 % of their diet consists of fruits (Kano and Mulavwa 1984; White 1992; Yamagiwa 2004). The amount of meat consumption is not as high as in some chimpanzee populations but seems to fall within the general range of chimpanzees. Bonobos (including females) hunt small mammals, usually solitarily (Fruth and Hohmann 2002; Surbeck and Hohmann 2008).

In Wamba as well as in Lomako, the home ranges of communities overlap extensively (Idani 1990; Hohmann and Fruth 2002). Their size lies between 22 and 58 km^2 in Wamba (Idani 1990). Each adult has an individual home range or core area within the community's home range (White 1996).

Bonobos may experience lower leopard predation pressure than chimpanzees because they spend more time off the ground (Boesch 1991). Outside the forest, they seem to be very careful; if they feed on fruit in the grassland, they remain quiet (Myers Thompson 2002).

Life Histories and Dispersal

Bonobo infants are weaned at 3–4 years of age, and the interbirth interval is about 4–7 years (Lee 1999; Yamagiwa 2004). Females conceive for the first time at about 10–14 years. Adult males have a mean weight of 39.2 kg, and females weigh 31.5 kg (Groves 1986).

Females transfer to other communities as older juveniles or early adolescents (Furuichi 1989). Paternity analyses suggest that there must be a large exchange of females between communities (Gerloff et al. 1999). Males tend to stay in their natal community. Occasionally, they may transfer to other communities, but this is rare (Hohmann 2001).

Size and Structure of Social Units

Much like common chimpanzees, bonobos live in a fission-fusion social system. Parties usually contain mature individuals of both sexes with more females than males. The proportion of all-female parties in Lomako is high and of all-male parties low (Hohmann and Fruth 2002). If estrous females are present, the proportion of males increases (Hohmann and Fruth 2002). Lone individuals are rare – usually males travel alone (White 1996).

Party sizes are determined by food availability: if more fruits are available and if the food patch is large, the parties grow larger. Males disperse when food becomes scarce, but females do not (White 1998; Furuichi et al. 2008). As bonobo food includes herbaceous plants that are abundant in the rain forest during all seasons, feeding competition is low.

In general, bonobo parties are large in Lomako and Wamba, compared to chimpanzees. While chimpanzee parties are 9–21 % of the community size, bonobo parties consist of 21–89 % of the community. Bonobo parties last longer than those of the chimpanzees at Taï and Gombe (in Wamba 86 min, in Lomako 102 min; Boesch and Boesch-Achermann 2000).

Community sizes in Wamba are very variable, ranging from 33 to more than 100 members (Idani 1990). The cohesion of community members is high, and they stay together most of the time. In Lomako, several parties may congregate in the evening to nest in proximity to each other (Hohmann and Fruth 2002). Community members may be separated by kilometers for days or weeks (White 1996).

Male-Female Relationships and Mating Strategies

It is usually stated that in bonobo communities, either females are dominant over males or both sexes are codominant/egalitarian (Gerloff et al. 1999), but recent studies suggest that males dominate females – except for feeding situations (White and Wood 2007). Long-term bonds are found predominantly between heterosexual dyads and involve not only close kin but also unrelated individuals. Relatives associate and groom more often, however, and kinship ties are important between males and females. The highest association rates are observed between adult females and their adult sons: males receive agonistic aid from their mothers in conflicts with other males (Hohmann et al. 1999; Kapsalis 2004). Aggression by males toward females is less intense than in chimpanzees. Females may form alliances to attack males (Furuichi 1989; Hohmann and Fruth 2002).

Bonobo mating is opportunistic and promiscuous and involves no or little aggression between males. The maximal swelling lasts for a large proportion of the cycle; therefore, males establish long-term bonds with females that exceed tumescence (Fruth et al. 1999). Nevertheless, sexual coercion is found in some populations; high-ranking males have a strong tendency to monopolize tumescent females and they sire more offspring (Kano 1996; Gerloff et al. 1999; White and Wood 2007; Surbeck et al. 2011). In low- and mid-ranking males, the mother's presence increases mating success (Surbeck et al. 2011).

Extracommunity copulations are not uncommon, and females are rarely prevented from mating with members of neighboring communities. The number of infants sired by nonresident males is low; more than 80 % of the infants in Lomako are fathered by resident males. No infanticide was observed so far in bonobos (Fruth et al. 1999; Gerloff et al. 1999).

Female-Female Relationships

Female bonobos are more affiliative and cohesive with each other than chimpanzees. Contact frequencies between females are higher than between females and males or between males. They associate and forage in larger parties for most of the year, share food, and support each other in food defense (Hohmann and Fruth 2002). These affiliative bonds are not particularly observed between related females; female associations are not based on kinship (Kapsalis 2004).

Female bonobos groom less than male-male and male-female dyads but show a unique behavior called genito-genital rubbing, especially in the context of feeding: two females embrace each other ventro-ventrally and rub their genital swellings together with rapid sideways movements. The function of this behavior was discussed by various authors, such as Hohmann and Fruth (2000), who observed genito-genital rubbing six times as often as female-female aggression. According to their analysis it serves reconciliation and tension regulation.

Male-Male Relationships

Although strong bonds between males exist, especially at Wamba, they are less prominent than the bonds among females (Hohmann and Fruth 2002). Unlike chimpanzee males, bonobo males have even fewer contacts with other males than with females (White 1998). High-association rates are observed between maternally related adult brothers (Kapsalis 2004). Alliances are unusual between males (Hohmann et al. 1999). The males establish dominance relationships with each other, but aggression is less intense than in chimpanzees and conflicts are often settled in a nonagonistic way (Hohmann and Fruth 2002; Surbeck et al. 2011).

Intergroup Interactions

Bonobo communities do not seem to search for and contact neighboring communities. Lomako males have never been seen to make border patrols (Hohmann and Fruth 2002). In Wamba, intergroup encounters vary from group fights to peaceful intermingling. In general, encounters are peaceful and communities may spend hours together. Females take the initiative in the temporary fusion of communities. During these community meetings, males keep a certain distance from the males of the other group. The most prominent form of intergroup interaction between males and females is copulation, and relations between resident and unknown females are characterized by friendly contacts (Idani 1990; Kano 1996; Gerloff et al. 1999).

There are frequently aggressive interactions between males when they approach, but direct body contact and cooperative attacks are rare; the aggressive interactions are never as fierce as those reported for chimpanzees (Idani 1990; Hohmann and Fruth 2002). Agonistic aid during conflicts between members of different communities has never been reported. Severe aggression does occur, however, when mixed-sex parties encounter unknown males; in such a case, the strangers are charged by the males and also by the females (Hohmann et al. 1999). No fatal aggression was observed between bonobo communities at Wamba (Kano 1996).

Discussion: Genus *Pan*

Usually the chimpanzee social system has been regarded as male-bonded, with strong kinship ties between the males of a community but no relationships between the females. Experience from various field sites does not always support this idea and indicates that it is much more complicated and variable. In Taï, males within a community are on average not significantly more related than females, and the group members have more relatives within their home community than outside (Vigilant et al. 2001). Association patterns do not support the view of strong bonds between males in general (Pepper et al. 1999).

Taï chimpanzees may be bisexually bonded, while other populations are male-bonded, and more cooperation is found in Taï than in eastern chimpanzees. The reasons are presumably differences in habitat. Boesch and Boesch-Achermann (2000) assume that the forest environment allows or forces bonobos and chimpanzees to build larger and more cohesive parties. Doran et al. (2002b) hypothesize that permanent female association with males is a female counterstrategy to infanticide risk and that more infanticide occurs in habitats with considerable annual variance in fruit production. Bonobos live in a still more stable environment than Taï chimpanzees – this may lead to even more stable party sizes (Doran 1997). Bonobo parties seem to be large compared to chimpanzees (Table 3), but the within-species variation is larger than the interspecies variation (Hohmann and Fruth 2002; Furuichi 2009).

Bonobo communities seem to be composed of unrelated females who are highly affiliative with each other and related males who are not highly affiliative with each other; females directly control competition with homosexual behavior (Boesch and Boesch-Achermann 2000). Aggression between males and between the sexes is less intense than in chimpanzees, and conflicts are often settled in a nonagonistic way. Bonobos in general have more relaxed relationships than chimpanzees that do not depend on kinship, as paternity studies show that there is no matrilineal organization (Gerloff et al. 1999).

The typical chimpanzee/bonobo social structure is a multimale group with a fission-fusion structure. Similarities are obvious with respect to party size and association patterns. Female bonding in bonobos does not exceed that of some chimpanzee populations; differences between the two species are the proportion of female party members and the frequency of mixed parties (Hohmann and Fruth 2002). Chimpanzees as well as bonobos have the potential for great social variability, with considerable capacity for cooperation, reciprocal interactions, and coalitional behavior (Boesch and Boesch-Achermann 2000).

Despite the common basis, the two species show some differences in social behavior. Wrangham et al. (1996) think that this can partly be explained by the differences in feeding competition: chimpanzees and gorillas live sympatrically in many areas while bonobos do not have a great ape competitor.

Sympatric Ape Populations

Sympatric apes share a great part of their diet – in Asia as well as in Africa (Morgan and Sanz 2006; Vogel et al. 2009; Yamagiwa et al. 2012). This is especially visible in fruits. Sugardjito et al. (1987) observed some competition between orangutans and siamangs in Gunung Leuser, and one benefit of grouping for Sumatran orangutans may be that siamangs cannot drive the youngsters away from fruiting trees. More obvious, however, is the interspecific competition between chimpanzees and gorillas in Africa.

The dietary overlap between gorillas and chimpanzees ranges from about 50 % at Kahuzi-Biega to 60–80 % at Lopé and Ndoki. In Kahuzi-Biega, all fruit species eaten by gorillas are also eaten by chimpanzees. Overt interspecific competition between chimpanzees and gorillas has not been observed at any site; instead, competition avoidance is commonly seen (Kuroda et al. 1996; Morgan and Sanz 2006; Head et al. 2011). Interspecies relationships are more peaceful than intergroup relationships within the two species (Yamagiwa et al. 2003b). In Gabon, Okayasu (2004) observed close interactions between gorillas and chimpanzees; occasionally the groups would mix and play and even sleep at the same site.

During fruit scarcity, gorillas increase the proportion of herbaceous vegetation in their diet, while chimpanzees as obligatory frugivores continue to search for fruit. The two species obviously find different niches (Yamagiwa et al. 2003b, 2012), and some habitats are used almost exclusively by one species (Tutin and Fernandez 1993; Malenky et al. 1994; Kuroda et al. 1996; Rogers et al. 2004).

Kuroda et al. (1996) suggest that the low population densities of gorillas and chimpanzees in Lopé and Kahuzi-Biega might partly be due to competition. Possibly interspecific competition over food affects foraging strategies and may have caused divergence in grouping patterns. The larger party sizes of bonobos are possible because of the high density of terrestrial herbaceous vegetation; as gorillas mainly eat these plants, sympatric chimpanzees may be forced to take a different foraging strategy and to form smaller parties (Wrangham et al. 1996; Yamagiwa and Takenoshita 2004). The effects of competition have not been analyzed yet, but they are difficult to study – also because additional competitors like elephants have to be considered (Rogers et al. 2004).

Conclusions and the Genus *Homo*

Although some great ape populations have been studied for decades, their social systems are not yet completely understood. The Asian apes seem to be less social than the African apes; this may be due to food types and distributions in Southeast Asian forest, which may differ strongly from African forests. All great apes lead “individual-centered lives,” but they need interaction with familiar conspecifics. Despite their tendency to congregate, their social structure is characterized by weak ties, compared to female philopatric primates.

Female transfer is common to all species. They have a tendency toward fission-fusion grouping; females lack sharply defined dominance relations, and intrasexual bonds among non-kin can be relatively strong. Van Noordwijk et al. (2012) hypothesize that this ability to form and maintain bonds has freed females from the necessity to be strictly philopatric. It is difficult to assign a social system to each ape species (or to the family Hominidae in general) because there is remarkable intraspecific variability in social organization and structure. Especially frugivory requires a mobile and flexible population.

Compared to the great apes, humans show an even greater variability in social structure – nevertheless, there are certain trends across all human societies (Rodseth et al. 1991): males maintain consanguineal kin ties; females maintain consanguineal kin ties; males cooperate in conflicts against other males; and females also cooperate but rarely in physical conflicts with other females.

According to Knauft (1991), simple human societies are decentralized, and there tends to be active and assiduous devaluation of adult male status differentiation. Among complex hunter-gatherers and with the advent of sedentism and horticulture/agriculture, male status differentiation increased. There seems to be a similarity between great apes and middle-range human societies in terms of competitive male dominance hierarchies. Such dominance relations may not be particularly adaptive in environments of low resource density and predictability; this may have led to the simple egalitarian hunter-gatherer societies that nowadays live in extreme environments.

Most human societies are characterized by female-biased dispersal and male philopatry. Long-term pair bonds between males and females are common, although their form, strength, and duration vary between societies. Moreover, these bonds are not identical with mating and grouping patterns (Pusey 2001). And according to the cooperative breeding model, these bonds allowed the increase of brain size during the development of *Homo* (Hrdy 2005; van Schaik and Burkart 2010; Isler and van Schaik 2012).

There has been much speculation on the "natural" human mating system. Although fossils of man's early ancestors show extreme sexual dimorphism, modern human males are only about 15 % larger than females; the relative size of testes in humans is much smaller than in chimpanzees and comparable to "monogamous" or one-male group species. Polygamy with only some males producing many offspring thus cannot be the common mating system in humans, but social monogamy is not common either (Low 2003). According to Plavcan (2012) size dimorphism is not a robust indicator for breeding systems.

The social system of humans certainly has several levels, like the social system of *Pan* (Layton et al. 2012). Dunbar (1993) developed the hypothesis that there is a species-specific upper limit to group size that is set by cognitive constraints. This would mean that human groups can be much larger than those of the great apes. According to Dunbar, group size depends on the maximum number of individuals with whom an individual can maintain personal contact. He discerns (in modern hunter-gatherer societies) the group levels overnight camp (30–50 members), band/village (100–200 members), and tribe (1,000–2,000 members). Dunbar's overnight camp certainly is not the smallest human grouping above the individual. Rodseth et al. (1991) and Pusey (2001) state that the majority of human societies consist of conjugal families united in stable communities, but also relatively autonomous families. Apart from these units, associations of men usually play an important role too (Rodseth 2012).

But what is the central, stable component of the human social system? Even ape specialists have contradictory opinions. De Waal (2001) thinks that the nuclear family is the basic social grouping of humans and that this unit is unique to the species *Homo sapiens*, although Low (2003) states that it is rather unusual in human societies. Perhaps the nuclear family is an especially successful social structure in modern industrialized societies. Ghiglieri (1989) calls the social structure of humans a multimale kin group, a stable, semiclosed fission-fusion community.

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Evolutionary Biology of Ape and Monkey Feeding and Nutrition

Joanna E. Lambert

Contents

Abstract

Like all animals, primates must garner sufficient energy and nutrients from their habitat to accomplish other biological imperatives such as mating and avoiding predators. The order Primates exhibits an extraordinary diversity of feeding and foraging-related adaptations to meet this imperative, some of which are shared with other taxa, others of which are unique to primates. In this chapter, I explore the evolutionary underpinnings of these adaptations as well as evaluate their ecological implications. I first discuss several unique aspects of primate feeding biology, including the evolution of large brains, trichromatic color vision, and tool use. I then move on to evaluate the fundamental problems of plant fiber and chemical defenses and conclude by arguing that primate adaptations for

J.E. Lambert (✉)
The University of Texas, San Antonio, TX, USA
e-mail: joanna.lambert@utsa.edu

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fermenting fiber and detoxifying plant chemical defenses have implications for primate species adaptations, abundance, and richness since the Miocene. Because of the implications for understanding adaptations in our own lineage, in this latter section I pay particular attention to Catarrhini of Africa; I employ a strongly comparative approach and evaluate hominoid feeding biology in light of what we know about Cercopithecoidea.

Introduction

Feeding is a biological imperative. Like all animals, primates must garner sufficient energy and nutrients from their habitat to accomplish other biological imperatives such as mating and avoiding predators. This rather obvious fact has not gone unnoticed by primate biologists and inquiries into how and what primates consume have been central to primate studies since the 1970s (Clutton-Brock 1977; Chivers et al. 1984; Rodman and Cant 1984; Altmann 1998).

Most primates are omnivorous and, by definition, consume both plant and animal matter. Nonetheless, primate requirements for energy and nutrients are met largely by plants (Milton 1993). The system of energy transfer from plants to animals via herbivory evolved during the Permian, ca. 255 Myr.This is the food chain with which we are most familiar [i.e., producer (plants) to primary consumer (herbivores) to secondary consumer (carnivores)]; the addition of an herbivore trophic level represents a marked shift from previous time periods that lacked primary consumers (Potts 1996). This changed dramatically throughout the Mesozoic as angiosperms (flowering plants) evolved and as amphibians, reptiles, and eventually mammals radiated into a diversity of plant-consuming niches. Primates is thus among these modern orders that evolved to feed primarily from the kingdom Plantae, and they do so with staggering diversity in their foraging and feeding adaptations. Indeed, extant primates forage in literally every possible social permutation: as solitary animals, as mated pairs, in feeding parties that fission and fuse, and in cohesive social groups (Strier 2010). Primates procure food in a diversity of ways as well, and there is virtually nothing that some primate species will not eat, from fungi and lichen, grass and palm nuts, and nectar and termites to snakes and antelopes. Accordingly, primates exhibit a diversity of feeding-related morphological adaptations in dentition, digestion, locomotor apparatus, and myriad cranial and postcranial features.

Evolution is a wondrous thing, resulting in adaptations that are unique to species (autapomorphies), shared by several related taxa (usually synapomorphies but sometimes homoplasies) or inherited from an original, ancestral state (plesiomorphy). Moreover, "natural selection, acting in various guises at various levels, seems together with genetic drift to account for almost all features of organisms once the appropriate raw material has arisen by mutation and recombination" (Futuyma 1979, p. 438). Hence, we can assume that feeding-related features observed in primate species today are (1) the result of natural selection and other microevolutionary forces and are either (2) unique to a species (e.g., mandibular morphology), shared by a subset of primate taxa (e.g., cercopithecine cheek pouches), shared by all primates (e.g., postorbital bar), or are ancestral to mammals (e.g., heterodonty) or animals generally (e.g., reliance on ingestion).

Given this extraordinary diversity at multiple scales, I cannot do justice to the entire array of strategies employed by primate species for procuring nutrients from their environments (for more information, see Garber 1987; Milton 1993; Janson and Chapman 1999; Lambert 2011; Chapman et al. 2013). Instead, my focus here is to first evaluate several noteworthy – indeed, unique to the order – aspects of primate feeding biology. Thus, in the first part of this chapter, I evaluate the feeding implications of large brains, trichromatic color vision, and tool use in primates. I next discuss the fundamental problem, shared by all plant-consuming animals, of plant fiber and chemical defenses. I conclude by arguing that primate adaptations for fermenting fiber and detoxifying plant chemical defenses have had implications for primate species adaptations, abundance, and richness since the Miocene. While primates encounter such feeding challenges in all biogeographic areas in which they are found, because of the implications for understanding adaptations in our own lineage, I pay particular attention to the Catarrhini of Africa. I employ a strongly comparative approach and evaluate hominoid feeding biology in light of what we know about Cercopithecoidea.

Feeding Adaptations Unique to Primates: Evolution of Large Brains, Color Vision, and Tool Use

Roughly three-fourths of all primate species forage and feed in cohesive social groups (Strier 2010). The observed size of a primate social group is generally expected to be one that is big enough to provide protection from predators while concomitantly small enough that group members do not incur too great a cost from increasing feeding competition (Struhsaker 1981; Terborgh and Janson 1986; Dunbar 1988; Garber 1988; Janson and van Schaik 1988; van Schaik 1989; Chapman 1990; Isbell 1991; Janson 1992; van Schaik and Kappeler 1993; Chapman et al. 1995; Janson and Goldsmith 1995; Treves and Chapman 1996; Sterck et al. 1997; Boinski et al. 2000; Chapman and Chapman 2002; Koenig 2002; Snaith and Chapman 2007). As a consequence of extreme variability in food availability in different habitats, primate species and populations experience the cost of feeding competition to varying degrees (Snaith and Chapman 2007).

Regardless of the degree to which primates do or do not compete for food, they must meet their basic nutritional needs for macronutrients (carbohydrates, protein, lipids) and micronutrients (vitamins, minerals, and water). Primates require the full suite of nutrients needed by mammals in general (45–47 in total of amino acids, fatty acids, vitamins, and minerals); large quantities of macronutrients are required for energy related to growth and maintenance, while micronutrients are vitally important for innumerable physiological processes (Oftedal and Allen 1996; Leonard 2000). In meeting these needs, primates are confronted with an array of feeding challenges that influence food quality. These challenges can be intrinsic, representing some inherent chemical, nutritional, or structural feature of the food, or extrinsic, a function of availability of that food and the costs (e.g., increased ranging, competition) associated with feeding on it as a consequence of that availability (Lambert 2011). Primates are not unique in having to deal with feeding challenges, but several (characteristically primate) adaptations are particularly deserving of further discussion because of their significance to feeding: brain expansion, trichromatic color vision, and tool use.

Brains

"The most distinctive characteristic of primates is the size and complexity of the brain" (Napier and Napier 1985, p. 34). In making this comment, the Napiers echoed the work of Le Gros Clark (1959) who argued that the extreme neocortical expansion observed in modern humans is a continuation of a trend in mammals in general (whose brains are on average 10× larger than those of reptiles) and primates in particular (Deaner et al. 2007; Dunbar and Shultz 2007). Indeed, primates as an order have a brain that is 2× larger than what would be expected of mammals of a particular body size, apes roughly 3–4×, and modern humans 7–8× (Jerison 1973; Martin 1996). The increase in brain size is particularly notable in the neocortex and especially in those areas of the brain concerned with vision and higher functioning (Radinsky 1977; Martin 1990).

It is thus not surprising that discussions regarding primate evolution generally – and human evolution specifically – almost invariably center on the biological and ecological variables that may have been of particular selective importance in the evolution of brain size (Dunbar and Shultz 2007). Given that, in addition to being the most encephalized, primates are also among the most social of mammals, a number of hypotheses regarding brain expansion have centered on the cognitive demands of negotiating and maintaining complicated social relationships (Byrne and Whiten 1988; Dunbar 1992; Barton 2000; Dunbar and Shultz 2007). Others, however, are focused on the relationships among brain size, metabolism, and dietary quality, while still others have evaluated the role of foraging in ecologically complex landscapes in selecting cognitive capacity (Milton 1988; Aiello and Wheeler 1995; Garber 2000). These scenarios (i.e., sociality versus diet or ecology selecting for brain size) are not necessarily mutually exclusive (Dunbar and Shultz 2007). Indeed, the social brain hypothesis has sometimes been interpreted as though it was ecology-free and represented a contrast between ecology and sociality as the driving force of brain evolution. This is possibly because, in the original analyses (Dunbar 1992), sociality was pitted against a set of alternative ecological hypotheses. It is important to remember that the social brain hypothesis is itself an "ecological hypothesis" (Dunbar and Shultz 2007, p. 650).

Brain tissue is metabolically expensive and requires more energy (in the form of glucose) than any other tissue in the body (Aiello and Wheeler 1995; Isler and van Schaik 2006; Barrickman et al. 2008). There are also differences in total number of neurons and relative brain size among primate species, suggesting differences in energetic demands (Fonseca-Azevedo and Herculano-Houzel 2012). Although earlier analyses (e.g., McNab and Eisenberg 1989) suggested no correlation between relative brain size and basal metabolic rates (BMR) in mammals, more recent work (Martin 1998; Isler and van Schaik 2006; Fonseca-Azevedo and Herculano-Houzel 2012) suggests that after correcting for phylogeny and body size effects, BMR and brain mass correlate positively and energy requirements scale linearly with total number of neurons. It has thus been hypothesized ("expensive -tissue hypothesis") that the metabolic expense of maintaining a large brain is offset by a reduction in other energetically expensive tissues, especially the digestive tract (Aiello and Wheeler 1995). Navarrete et al. (2011) recently tested this hypothesis. In a sample of brain size and organ mass that included 100 mammal species (23 primates), these authors found that there was no evident negative correlation with brain size or gut mass – or any other organs. However, they did find that brain size and adipose storage depots are negatively correlated. While these results do not support the expensive-tissue hypothesis directly, they are consistent with a broader "energy-based hypothesis," as encephalization and fat storage are alternative strategies for buffering against energy deficits (Navarrete et al. 2011).

While an energetic trade-off in total mass of digestive and brain tissue has received mixed support, it is evident that gastrointestinal morphology and proportions are reasonably predictable of the nutrient density and "packaging" (sensu Altmann 2009) of foods that primates consume. Chivers and Hladik (1980), for example, determined that mammals relying primarily on vertebrate prey have a simple stomach, an unspecialized colon, and a long, complex small intestine. In contrast, species relying heavily on vegetative plant parts are typically characterized in having large chambers (stomach, cecum, colon) in the gut for fermenting structural carbohydrates (fiber), while mammals that rely on fruit are noted for their relatively unspecialized gut. Differences in gut morphology among frugivores are generally attributed to the degree to which each species relies on either insects or leaves for protein to supplement its fruit diet.

Relatively more encephalized primate species have also been noted to be those primate species with a more nutrient dense and readily digestible diet (Milton 1988; Aiello and Wheeler 1995; Navarrete et al. 2011). Foods differ widely both in nutrient density and in their digestibility, and some require more digestive processing (either by endogenous enzymes or by microbial fermentation) than others before energy is yielded (Lambert 1998). Fruit, for example, while exhibiting wide interspecific variation, is generally a source of easily digested, nonstructural carbohydrates (esp. fructose), and leaves tend to be higher in structural polysaccharides (fiber) and require more time and digestion before energy is yielded. Insects (both mature and larval) can be a good source of protein and lipids, although the costs of searching and handling time and the polysaccharides of chitinous exoskeletons mitigate net energy yield and digestibility. Meat from vertebrate animals is an excellent source of protein and fats and is easily digested (by the action of pepsin, trypsin, and chymotrypsin in the stomach; Tortora and Anagnostakos 1987).

The concomitant facts that modern humans have the largest relative brain size among animals, a simple and relatively small total gut for their body size, and an evolutionary history of meat consumption are of considerable interest to paleoanthropologists and primate feeding biologists alike (see chapter "▶ Evolution of the Primate Brain," Vol. 2). Indeed, with regard to human evolution, Milton (1999) has argued that: "by routinely including animal protein in their diet, they [i.e., humans] were able to reap some nutritional advantages enjoyed by carnivores, even though they have features of gut anatomy and digestive kinetics of herbivores" (p. 11). In other words, by increasingly including meat (a readily digested food) in the diet, our human ancestors garnered the requisite energy for maintaining an increase in body size while at the same time evolving a larger brain at the expense of total gut size (Aiello and Wheeler 1995; Milton 1999).

Some scholars have also noted the relationships among brain size, cognitive capacity, and food distribution and availability (Milton 1988; Dunbar and Shultz 2007; Taylor and van Schaik 2007). As mentioned, primates consume a broad diversity of food types, largely of plant origin, and to a lesser degree of invertebrate and vertebrate animals. For ease of discussion, plant foods are often lumped into broad feeding categories, including vegetative plant parts (e.g., leaves) and reproductive plant parts (e.g., fruit, seeds, flowers). Vegetative and reproductive plant foods in a habitat are distributed neither evenly nor equally in space and time, and there is wide variation within and between habitats and species in their richness, abundance, and nutritional quality. Consequently, the initial challenge to all animal consumers is finding food in the first place: not an insignificant task (Oates 1987; White 1998). "Typical" habitats do not exist, and generally speaking, primate food resources are difficult to find (Milton 1988; Janson and Chapman 1999). Indeed, in an analysis of tree abundance in Barro Colorado Island, Panama, Milton (1988) found that 65 % of all tree species were encountered less than once per hectare and ripe fruits were available for individual trees only 0.8 months/annum. Nonetheless, there are gross differences in availability among broad food types, and, for example, within a given habitat, vegetative plant parts such as mature leaves tend to be more abundant and predictably available relative to reproductive plant parts such as fruits, seeds, flowers, and nectar which are more patchy in space and time (Milton 1980; Isbell 1991). This is a function of the fact that most tropical forests are characterized by tree species with differences in seasonal and annual fruit production and by trees that either produce fruit in small quantities or produce abundant fruit in widely scattered trees (Janzen 1967; Frankie et al. 1974; Whitmore 1990; van Schaik et al. 1993).

That primate foods differ in their distribution and availability suggests differing selective pressures with regard to cognitive capacity: some foods are intrinsically more difficult to monitor and locate than others (Garber 2004). Parker and Gibson (1977), for example, suggested that large brain size correlates with omnivorous feeding in primates. Milton's (1988) long-term research on *Alouatta palliata* (mantled howler monkeys) and *Ateles geoffroyi* (spider monkey) identified important differences in foraging and feeding that also correspond to brain size. The relatively small-brained howler monkey, while at times of the year highly frugivorous, in general relies heavily on leaves, which are both more abundantly distributed and more refractory to digestion than fruit. During some seasons, howler monkeys can spend upward of 90 % of daily feeding time on leaves. Conversely, the relatively larger-brained spider monkey is highly frugivorous and spends an annual average of 72 % daily feeding time on fruit. The overall differences in time devoted to fruit versus leaves and in distribution and availability of vegetative and reproductive plant parts are reflected in total home range size of the two species: 31 ha in howler monkeys and 800 ha in spider monkeys. Thus, Milton argues (1988, p. 289) that: “spider monkeys are faced with a far more complex problem than howlers with respect to locating their food sources since, in effect, they are dealing with a supplying area over 25 times as large.” A more patchily distributed food source requires greater cognitive capacities for dealing with a more complex ecological matrix. Spider monkeys exhibit a relative brain size and degree of neural complexity approximately 2× that of howler monkeys (*Ateles* body size: 7.6; brain weight: 107 g; *Alouatta* body size: 6.2 kg; brain weight: 28 g). And while it is recognized that indices of relative brain size are not necessarily direct indicators of cognitive capacity, in this case Milton (1988) argues that it does appear that selective pressure for spatial memory is more intense for spider monkeys (a frugivore) than howler monkeys (a folivore), which too may help to explain differences in gross brain size and complexity.

Along these lines, Potts (2004) has posited a “fruit-habitat hypothesis” suggesting the evolution of the large relative brain size and concomitant cognitive capacity among great apes can be explained by a “causal connection between ape ancestral diets, habitats, and environmental history” (p. 224). In short, he argues that as preferred fruit resources became increasingly rare as a function of forest reductions and climatic shifts in the African Miocene, ancestral apes were under extreme selective pressure for evolving cognitive means (e.g., complex mental representational ability) to deal with food source uncertainty.

More recently, Taylor and van Schaik (2007) explained differences in brain mass among orangutan populations in terms of habitat quality and food availability and explicitly integrated ideas related to the energetics of encephalization. Using cranial capacity (CC) as an index of brain mass, these authors found – after adjusting for body size – significant variation in CC in populations of *Pongo pygmaeus* and *P. abelii*. *Pongo pygmaeus morio* had a significantly smaller CC than any other orangutan population and is also found in the least productive habitat – regularly undergoing food scarcity and lean periods. The authors suggest their results are consistent with the hypothesis that decreased brain mass can be explained in part by overall habitat quality, diet, and access to energy.

Other feeding-related features, such as extractive foraging, have been linked to relative brain size (Barton 2000). For example, members of the most encephalized platyrrhine genus, *Cebus*, are highly manipulative, destructive foragers and are highly adept at extracting resources from tree cavities, as well as difficult to penetrate food types such as hard palm nuts. The aye-aye (*Daubentonia madagascariensis*) is among the most encephalized prosimian species, and a majority of its calories are derived from arthropod grubs that they have extracted deep from within branches. Common chimpanzees in dry savanna habitats are known to use spears to extract prey from within tree cavities and fishing wands to extract termites from otherwise impenetrable termite nests (Pruetz and Bertolani 2007; more on these examples in the subsequent section on "Tool Use").

Trichromatic Color Vision

Primates exhibit a diversity of visual adaptations that distinguish them from other mammals, several of which have been related directly to feeding and foraging. Primates, for example, have very large eyes relative to body size and a high degree of orbital convergence; both traits are argued to be of selective advantage for nocturnal visual predation (Cartmill 1992; Ross 2000). Primates, too, are unique among mammals in having trichromatic color vision. Color vision relies on the presence of photoreceptors that contain light-sensitive opsin proteins (cones). Most vertebrates (including reptiles, birds, and some fish) have four such photoreceptors (hence, "tetrachromacy"), each with different peak light spectral sensitivity (Ross 2000; Dominy 2004; Dominy et al. 2004; Jacobs 2008). However, early in the radiation of mammals, at least two of these photoreceptors were lost, the legacy of which is that most extant Eutherian mammals have only two opsin proteins, resulting in dichromatic color vision. This is often explained by the fact that the earliest niche occupied by mammals was a nocturnal one; since cones perform poorly under low-light conditions, the selection for their maintenance was relaxed (Jacobs 2008). Although, it is noteworthy that most recently Melin et al. (2013) have suggested that the anthropoid visual system – including the L/M opsin gene – evolved under low-light conditions and challenges the perspective that while basal primates were nocturnal, stem anthropoids were diurnal (see chapter "▶ Primate Origins and Supraordinal Relationships: Morphological Evidence," Vol. 2).

It is of considerable interest that in Primates, trichromacy has not only evolved once but potentially several times. The primitive mammalian condition includes one short-wave (430 nm, "S") and one long-wave (560 nm "L") sensitive cone pigment, with the long-wave pigment gene located on the X-chromosome. Subsequent gene duplications on the X-chromosome in catarrhines resulted in separate middle-wave (530 nm, "M") and long-wave pigments; all cercopithecoids and hominoids tested to date exhibit the three cone opsins. Platyrrhines are highly variable in their perception of color, since there is a single X-chromosome locus for the opsin gene. With the exception of *Aotus* (a monochromat) and *Alouatta* (routinely trichromatic), all tested platyrrhines are polymorphic at the locus for the long-wave pigment and have mixed populations of dichromats (males and homozygous females) and trichromats (heterozygous females) (Ross 2000; Dominy 2004). Although the gene duplication in *Alouatta* is similar to that of Catarrhini, it is an independent evolutionary event and probably occurred quite recently (Jacobs 1996; Dominy 2004).

The combination of three opsins in the retina being tuned to different wavelengths facilitates perception of an enormous range of color hues, and there are multiple competing hypotheses regarding the selective pressure for the evolution of this visual system in primates. For example, Changizi et al. (2006) suggested that trichromacy was selected for discriminating important signals of sociosexual, threat, and emotional states via color modulation on the skin of conspecifics. Isbell (2006) has suggested that detection of a wide range of color hues (including along the red-orange channel) was selected for in pre-attentional visual perception of fearful stimuli such as snakes.

However, the fact that foods in natural habitats exhibit an equally large range of color has resulted in several feeding- and foraging-related hypotheses for the explanation of the evolution of color vision in primates. Generally, these hypotheses emphasize the advantages of color vision in detecting fruit, leaves, or both (Ridley 1894; Snodderley 1979; Lucas et al. 1998; Dominy 2004). For example, since at the least the turn of the century, it has been suggested that color vision is linked to the evolution of colorful fruit in angiosperms (Ridley 1894; Polyak 1957; Snodderley 1979; Regan et al. 1998). In this putatively coevolved relationship, flowering tree species evolved colorful fruit to ensure the attraction of seed dispersers (such as primates) and (some) primates became better at finding such fruit as a result of their trichromatic color vision.

There is no doubt that primates are important seed dispersers; as a taxon they are often the most abundant arboreal frugivores in tropical forests (Lambert 2002a; Lambert and Chapman 2005). Whether primate feeding has selected for fruit color and whether color vision coevolved with frugivory is much less clear. “Coevolution” is a narrowly defined process, wherein there is “an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response to the change in the first” (Janzen 1980, p. 611). As such, coevolution represents a highly specialized and interdependent step-by-step process of interrelated evolutionary change in two or more species and differs from both adaptation and exaptation in terms of the duration, strength, and mutual historical relationships between the interacting species.

In a detailed analysis of both catarrhine and platyrrhine frugivory and seed handling, Lambert and Garber (1998) found that primates in both allopatry and sympatry exploit a wide variety of plant species exhibiting a very broad and unpredictable array of fruit colors. Moreover, across taxa, these researchers found no evidence for any particular or consistent suite of fruit traits or patterns in the way fruits are processed and dispersed. Consistent with these findings, Dominy (2004) determined that primate frugivory is highly generalized with respect to hue and argues that rather than fruit color, it is either abundance or accessibility (or both) that is the more important determinant of fruit choice by primates. Moreover, the relationship between fruit color and nutritional properties (especially in terms of the sugar “reward”) is equivocal; hue and sugar are uncorrelated in Costa Rica and Peru (Wheelwright and Janson 1985; Dominy 2004). Nonetheless, the “old idea that primate trichromacy evolved in the context of fruit detection and identification enjoys some current support” (Jacobs 1996, p. 198).

Lucas et al. (1998) proposed an alternative hypothesis imputing leaf selection, rather than fruit, as the important agent of evolution for trichromacy.

As demonstrated by these researchers, leaf toughness is highly correlated with leaf color; toughness is also positively correlated with high fiber and negatively correlated with protein. These authors thus suggest that trichromatic vision may provide an important advantage in finding palatable and nutritious leaves in the tropics where many tree species delay the “greening” of leaves in an apparent attempt to ward off herbivores. In a study that focused on two colobine species, one cercopithecine, and one ape (*Pan troglodytes*) in the Kibale National Park, Uganda, Dominy and Lucas (2001) demonstrated that increasing reddishness of edible leaves is significantly correlated with reduced toughness and protein. Such a relationship was not found with fruit, and the fact that *Alouatta* – a folivore – is the only routine trichromat in the New World generally lends support to leaf-related hypothesis. The evolutionary context for trichromacy and its function in leaf detection may stem from early Anthropoidea. Climatologically, the Eocene-Oligocene transition is generally marked by dramatic cooling, which, in addition to many other ecological shifts, resulted in extinction or reduction in palms in Africa and Asia, although not in Madagascar or South America (Morley 2000; Dominy 2004). Dominy (2004) suggests with the loss of this critical keystone resource (i.e., palms), stem catarrhines turned to protein-rich young leaves; a chance mutation on the duplication of an opsin gene would have provided the underlying visual mechanism to exploit this new resource effectively. Primates in South America or Madagascar would not have been under such intense selection, given the availability of palms as an important resource.

However, social- and feeding-related selective pressures need not be mutually exclusive. Indeed, Fernandez and Morris (2007) have proposed a two-step process that involves both a foraging efficiency early phase and a sociosexual later phase. More specifically, they hypothesize that trichromacy in some primate lineages is the result of a preexisting bias (“exaptation” sensu Gould and Vrba 1982) for detection of red-orange that evolved for nonsocial, feeding purposes. Once evolved, trichromatism facilitated the sexual selection of red skin and hair that served as signals of emotional and sexual status.

Tool Use

Several animal species (e.g., sea otters, woodpecker finches, burrowing owls, naked mole rats, crows) have been noted for their use of objects in their environment and hence meet the definition of tool use: “the employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, organism, or the user itself” (Beck 1980, p. 10). Given this definition, tool use involves both an object of change and an agent of change (the tool) (Panger 2011). No species other than humans make tools to make tools (McGrew 1992), but tool use in nonhuman primates differs from that of other animals in several respects, including the long period of learning, the complexity of skills, the imputed cognitive abilities, and, in the case of common chimpanzees (*Pan troglodytes*), the diversity of tool kits and use of tool composites (Strier 2010).

Panger (1998, 2011) makes the distinction between *tool use* per se, which involves the manipulation of both an object and a tool, and *object manipulation*, which involves manipulation of only an object of change and not manipulation of the agent of change (e.g., licking objects, carrying objects while feeding).

Many species – both primate and non-primate – can be induced to use tools and manipulate objects in captive settings (Panger 2011). However, tool use is rare in nature (Garber 2004). Only *Homo sapiens* and common chimpanzees spontaneously and habitually (defined as the use of tools repeated by several individuals in a population over time) manufacture tools in the wild, orangutans (*Pongo*) less so (McGrew and Marchant 1992; Panger 2011). Bonobos (*Pan paniscus*), baboons (*Papio* spp.), and macaques (*Macaca* spp.) will use tools in the wild (although neither regularly nor habitually). The descriptions of *Cebus apella libidinosus* using hammer and anvil technology in dry forests of Brazil (Fragaszy et al. 2004; de Moura and Lee 2004) were of considerable interest to biological anthropologists not only because these were the first descriptions of routine tool use by a monkey species but also because stone tools were being used by a non-catarrhine taxon. Gorillas (*Gorilla* spp.) have yet to be observed using tools in the wild.

In most cases, primate tool use is undertaken within the context of feeding, the most famous example coming from Gombe National Park, Tanzania, where in 1960 Jane Goodall first observed and described chimpanzees extracting termites (*Macrotermes bellicosus*) from their mounds by using modified plant stems:

> Passages into a termite mound are narrow and not completely straight, so the materials used must be smooth and fairly pliable if they are to be effective. Tools are fashioned from grasses, vines, bark, twigs, or palm frondlets. Sometimes a chimpanzee will pick up almost any suitable material that is nearby, including the discard tools of others who have worked the mound previously. At other times clumps of grass, tangles of vines, and so on are carefully inspected before a tool is selected; a length may be picked, then discarded immediately before it has been used, and another choice made. To some extent the procedure reflects individual differences, but dry-season termiting call for more skill and more care in the choice of material that wet-season fishing, when (a) the insects are near the surface and (b) the soldiers are on the defensive and quick to bite at any foreign material inserted into the nest. (Goodall 1986, p. 536)

Pongo pygmaeus, too, has been observed to extract social insects (e.g., ants, termites) from crevices and holes in trees, as well as use twigs to pry seeds from *Neesia* spp. fruit (van Schaik and Fox 1996). In addition to fishing for termites and other social insects, the best-known feeding-related tool use in chimpanzees includes hammer and anvil technology for cracking open nuts. This form of tool use, wherein a stone or log is used as an anvil in combination with a rock hammer, is generally viewed as the most complex form of tool use in any nonhuman animal (Fragaszy et al. 2004). It is a tool composite ("two or more tools having different functions that are used sequentially and in association to achieve a single goal"; Sugiyama 1997, p. 25), and it involves employing multiple spatial relations in sequence.

Dramatic examples of tool use have been reported at the Fongoli chimpanzee research site in southeastern Senegal (Pruetz and Bertolani 2007). Between March

2005 and July 2006, Pruetz and Bertolani (2007) observed Fongoli chimpanzees craft and use spears to hunt lesser bush babies (*Galago senegalensis*). The manufacture and use of the spears involved multiple steps in a hierarchically organized sequence in which some steps could be omitted and others that were repeated. These steps include (1) locating the potential nest cavity in which the prey could be found, (2) locating a branch of appropriate size, (3) breaking off a tree branch and stripping off leaves and side branches, (4) removal of one or both ends of branch and/or bark, (5) stripping tip of tool, and (6) employing tool and then either discarding it and repeating steps 1–3 or enlarging the cavity opening in which prey is found. The number (and hierarchical nature) of steps undertaken by the Fongoli study subjects is indicative of a sophisticated level of planning and cognitive complexity hitherto assumed to only occur in hominids. The fact that females and immature chimpanzees hunt with spears more frequently than males has significant implications for interpreting the evolution of tool use in hunting in our own lineage (Pruetz and Bertolani 2007). Observations of using spears for hunting continue at Fongoli, as well as other remarkable behaviors such as cave use and evidence of a hominid-like concept of fire (Pruetz 2007; Pruetz and LaDuke 2009).

Marked contrasts in tool use and tool kits are found across populations of chimpanzees in Africa; some of these differences are clearly cultural, resulting from social traditions rather than ecological differences or availability of materials (McGrew 1992; Whiten et al. 1999, 2001). Hammer/anvil technology and spear use, for example, appear to be unique to West African populations of chimpanzees (Pruetz and Bertolani 2007). Although tool use by nonhuman primates, especially chimpanzees, differs in terms of what the tool is made of, how they are made, the contexts they are used in, and the tasks they are used for, a picture of their utility in dealing with food scarcity is beginning to emerge. As discussed previously, fruit as a primate food resource is particularly patchy both spatially and temporally. As it happens, the two primate taxa for which tool use is commonly reported (i.e., *P. troglodytes* and *Cebus* spp.) are also highly encephalized, highly frugivorous, extractive foragers. Fruit is an ephemeral resource and foraging frugivores must have strategies for dealing with those times of the year when their preferred foods are not available. In many cases, primate species "fall back" on alternate foods (e.g., bark, leaves, terrestrial herbaceous vegetation). If these resources are negatively correlated with the availability of preferred food, they then meet the definition for "fallback food" which are typically consumed in quantities that compensate for the scarcity of the animals' main foods (Gilbert 1980; Terborgh 1986; Lambert et al. 2004; Lambert 2007, 2009; Marshall and Wrangham 2007; Marshall et al 2009). Several authors have suggested that the use of tools during such periods may facilitate the use of fallback foods not otherwise available to them (Yamakoshi 1998; Fragaszy et al. 2004; de Moura and Lee 2004; Lambert 2007) and that tool use is a behavioral trait that is most likely to be selected for in extreme and marginal habitats.

The chimpanzee population at Fongoli, Senegal, is certainly supportive of this hypothesis; indeed, Fongoli is among the hottest, driest habitats in which chimpanzees occur (Pruetz and Bertolani 2007). As another example, the habituated chimpanzee community at Bossou, Guinea, lives in both a very small (5 km^2) and an isolated forest, leaving this community without the ability to either shift food types or expand their range in search of fallback foods (Yamakoshi 1998). Overall resource richness is low, and seasonality of fruit availability in this region of West Africa is extreme. Chimpanzees in this area employ a number of feeding-related tools, including hammer and anvil, pestle pounding, ant dipping, and algae scooping with leaves. Tool use in these chimpanzees facilitates the consumption of two important keystone resources: nut cracking for oil palm nuts and pestle pounding for oil palm pith. Both resources are heavily mechanically protected and cannot be exploited without the use of tools (Yamakoshi 1998). Similarly, de Moura and Lee (2004) have argued that "energy bottlenecks" create contexts for capuchins (*Cebus apella*) to derive benefits from tool technology. In the Caatinga dry forest of northeastern Brazil, capuchins have commonly been observed to use tools and do so during the extended dry season of this region. During such times, preferred foods are not available; resources that are available without tool use are not sufficient for nutritional requirements, and the capuchins forage terrestrially for tubers. Several tools and tool-facilitated behaviors have been found in four habituated capuchin groups foraging in these areas, including digging for tubers with stones, cracking open seeds and branches with stones, breaking tubers with stones, and using stones as hammers in combination with wooden anvils to crack seeds. These monkeys consume 41 plant foods; tool use increases the use of at least three of these plant species. The researchers argue that *Cebus* foraging for embedded resources in habitats that experience "energy bottlenecks" is facilitated by innovative tool use (de Moura and Lee 2004). A similar argument is made for *Cebus apella* in another dry region of Brazil, where capuchins commonly use hammer and anvil technology to crack nuts during the dry season when preferred resources are scarce (Fragaszy et al. 2004).

Such observations suggest that foraging-related tool use serves a critical function (sensu Rosenberger 1992; Kinzey 1978; Lambert et al. 2004; Lambert 2007), i.e., that, regardless of phenotypic variation (e.g., differences in cultural traditions), these behaviors were initially selected for during critical periods when other, more preferred foods are not available. This may have implications for understanding tool use in early human ancestors (Teaford and Ungar 2000) and can be understood in light of the work of Robinson and Wilson (1998), who have pointed that some resources are intrinsically easy to use and are widely preferred, while others require specialized features (in this case, tool use) on the part of the consumer. This allows consumers to exploit nonpreferred resources without compromising their ability to use preferred resources (Lambert 2007, 2009).

Primate Feeding Adaptations to a General Problem: Fiber and Plant Defense Chemicals

> The plant world is not colored green; it is colored morphine, caffeine, tannin, phenol, terpene, canavanine, latex, phytohaemagglutinin, oxalic acid, saponin, L-dopa, etc. We now hunger for the details. (Janzen 1978, p. 73)

The fact that primate evolutionary history is marked by plant consumption is not insignificant from a chemical perspective. Angiosperms have not been passive recipients of herbivory over the last 65 Myr; they have instead responded to predation by arming themselves with an extraordinary diversity of defensive chemicals (Harborne 1994; Iason et al. 2013). To date, approximately 100s of thousands of such chemical defenses have been identified, a number viewed to represent only a fraction of extant plant chemical diversity (Levin 1971, 1976; Freeland and Janzen 1974; McKey 1974; McKey et al. 1978; Rosenthal and Janzen 1979; Gartlan et al. 1980; Harborne 1994, 2002; references in Iason et al. 2013). In chemical defense, organic substances are accumulated in plant tissues in such a way that if they are consumed or tasted by an animal, feeding is deterred (Harborne 1994). Such substances may be bitter, have an unappealing odor, be poisonous, or have an antinutritional impact. These compounds are typically categorized into two broad categories: (1) digestion inhibitors, which interfere with the efficiency with which nutrients are obtained by the animal, and (2) true toxins, which are harmful to the animal in that they interfere with normal physiology and may result in death (Feeny 1976; Waterman and Mole 1994).

Because most chemical defenses are not directly involved in the primary processes of plant growth and reproduction, they are often collectively referred to as "secondary" compounds or secondary metabolites. However, some authors (Cork and Foley 1991) have argued that despite their roles in primary plant processes, complex structural carbohydrates (fiber) of plant cell walls should be considered defensive chemicals because of their antifeedant/antinutritional effects on consumers. Carbohydrates take the form of monosaccharide sugars, disaccharides, and polysaccharides (NRC 2003). The nonstarch polysaccharides are the fiber components of plant cell walls and can be further divided into the soluble nonstarch carbohydrates (soluble fiber) and the insoluble nonstarch polysaccharides (insoluble fiber). The insoluble, nonstarch polysaccharides comprise the structural components of the plant cell walls (hence, "structural polysaccharides") and include hemicellulose, cellulose, and lignin. Cellulose is the most abundantly distributed carbohydrate in the world (Sharon 1980) and represents a large proportion of the available energy content of plant foods (Blaxter 1962; Alexander 1993), although no vertebrate has the cellulose-digesting enzyme (cellulase) for breaking down this carbohydrate. The structural carbohydrates must instead be broken down in the gut with the assistance of fungi, protozoans, or, most commonly, bacterial symbionts in a process known as fermentation (Lambert 1998). Like cellulose, hemicellulose generally cannot be digested enzymatically but instead is broken down by fermentation (Milton and Demment 1988; NRC 2003). Lignin is completely unavailable to a primate consumer and is refractory to both endogenous enzymes and bacterial fermentation.

Primates have thus evolved in a chemically inhospitable environment and cannot simply consume any plant that they encounter. Stuart Altmann (2009, p. 615) sums up the issue perfectly: "For omnivorous primates, as for other selective omnivores, the array of potential foods in their home ranges present a twofold problem: not all nutrients are present in any food in the requisite amounts or proportions and not all toxins and other costs are absent. Costs and benefits are inextricably linked.

This so-called ‘packaging problem’ is particularly acute during periods, often seasonal, when the benefit-to-cost ratios of available foods are especially low.”

Indeed, there is ample evidence that primates are extremely selective feeders and consume only a fraction of the plant species available to them in a habitat (Oates 1977, 1987; Glander 1978; Milton 1984). Selective feeding behavior is also exhibited in terms of the times of day a primate will consume a given plant species (quantity/quality of toxins and antifeedants in a plant ebb and flow throughout the day), as well as which portions of the plant (e.g., leaf tips or petioles, but not the entire leaf), and the total quantity of a particular plant food that is consumed (Glander 1978; Struhsaker 1978; Oates 1987; Rothman et al. 2006; Altmann 2009; Lambert 2011; Chapman et al. 2013).

In addition to behavioral adaptations, like all herbivores primates have evolved an array of anatomical and physiological solutions for dealing with plant defenses. Alternative solutions to the “packaging problem” (sensu Altmann 2009) are well illustrated by the extant Cercopithecoidea (including Cercopithecinae and Colobinae) and the African Hominoidea. Here, I suggest that the ways in which these taxa ferment fiber and detoxify chemical defenses may have important implications for their abundance and diversity, both in the Miocene and today.

Making Sense of Dietary Differences: What Monkeys Eat, but Apes Do Not

The relationship between body mass and basal metabolism is a negatively allometric one. Smaller mammals thus require relatively more energy to maintain endothermic homeothermy, and larger mammals relatively less (Kleiber 1961; Bell 1971; Jarman 1974; Parra 1978; Gaulin 1979; Schmidt-Nielsen 1984, 1997; Martin 1990). This negative relationship can have important implications for diet, with smaller-bodied mammals generally expected to have relatively higher energetic requirements consumed than larger-bodied mammals (Bell 1971; Jarman 1974; Gaulin 1979).

Yet, contrary to what might be predicted by the so-called Jarman/Bell principle, wherever the diets of African apes have been studied in comparison to monkeys, apes are invariably called dietary specialists, relying on more nutrient-dense foods comprising less structural polysaccharides and toxins compared to sympatric, smaller-bodied cercopithecoids whose diets often include high levels of fiber and toxins (e.g., leaves, seeds, bark). For example, in Kibale National Park, Uganda, cercopithecines maintain a diverse diet at all times, whereas chimpanzees confine their diet almost exclusively to ripe fruit (Lambert 1997, 2002a, b, 2005; Wrangham et al. 1998; Watts et al. 2011a, b). When ripe fruit is scarce, chimpanzees either range further to procure ripe fruit or fall back on the pith of terrestrial herbaceous vegetation. Wrangham et al. (1998) have found that for every month studied over an 11-month period, sympatric chimpanzees had more ripe fruit in their diets than *Cercopithecus ascanius*, *Cercopithecus mitis*, and *Lophocebus albigena* and do not consume any more fiber in the diet than do these much smaller monkeys. Moreover, chimpanzees consume significantly less digestion inhibitors and toxins (e.g., condensed tannins, monoterpenoids, and triterpenoids) in their annual diet than cercopithecines.

This pattern holds for other African apes as well. Bonobos (*Pan paniscus*) focus most of their feeding time on ripe fruits (White 1998). On the basis of the research on mountain gorillas (*Gorilla gorilla beringei*), gorillas in general were long thought to be folivorous; it is now evident that this subspecies is only folivorous because of a complete lack of succulent fruit in their montane habitat. Indeed, Nishihara (1999) has found that western lowland gorillas (*Gorilla gorilla gorilla*) spend 63 % of their feeding time on fruit. And in a review comprising data from all long-term western lowland gorilla sites, Rogers et al. (2004) have found that these apes will maintain fruit in their diet throughout the year; the authors indeed call *G. g. gorilla* “fruit pursuers, with strong preferences for particular and often rare fruit species, for which they will incur significant foraging costs” (p. 175). Lowland gorillas are also highly selective when consuming vegetative plant foods and chose plant parts that contain the least fiber and tannin and most sugar (Remis et al. 2001).

While African apes focus on fruit, cercopithecines in general are noted for their eclectic diet and feeding flexibility (Rudran 1978; Struhsaker 1978; Gautier-Hion 1988; Beeson 1989; Richard et al. 1989; Maisels 1993; Chapman et al. 2002; Lambert 2002b; Altmann 2009). By the age of 1 year, *Papio cynocephalus* in Kenya, for example, have already ingested over 200 food types (Altmann 1998). Foods consumed by cercopithecines include those that are both readily digested and high in structural polysaccharides; they maintain a higher percentage of nonfruit plant parts in the diet – regardless of fruit abundance (Rudran 1978; Struhsaker 1978; Cords 1986; Kaplin et al. 1998; Lambert 2002b). In addition, as noted above, cercopithecines have long been noted for their capacity to consume plant foods with greater defensive chemical loads than those consumed by sympatric apes (Waser 1977; Andrews 1981; Conklin-Brittain et al. 1998; Wrangham et al. 1998; Lambert 2000, 2001).

Relative to cercopithecines, colobines are more dietarily restricted. These monkeys generally do not consume arthropods for dietary protein, and while some colobine species consume unripe fruit pulp, an alkaline forestomach pH (and the potential for acidosis) precludes colobines from consuming high levels of ripe fruit (Kay and Davies 1994). However, because of their specialized foregut fermentation strategy (see next section), colobines can very efficiently digest plant foods with high levels of both fiber and secondary metabolites not consumed by sympatric cercopithecines or apes (Kay and Davies 1994; Lambert 1998, 2002b; Lambert and Fellner 2012).

The dietary differences among monkeys and great apes of the Old World can be explained by alternative digestion, fermentation, and detoxification systems in Cercopithecoidea and African apes (Lambert and Fellner 2012).

Plant Fiber and Fermentation

The degree to which the nonlignin structural carbohydrates of plant cell walls can be used as a source of energy depends in part on the length of time that these components are retained in the fermenting chamber(s) of the gastrointestinal tract.

The two regions of the primate gastrointestinal tract that have undergone the most specialization for carbohydrate fermentation are the stomach and the large intestine (Chivers and Hladik 1980). In forestomach-fermenting primates, the primary fermentation chamber is a modified stomach. Members of the subfamily Colobinae are unique among primates in having this fermentation system (Kay and Davies 1994). Their specialized, complex stomach is divided into three or four chambers; diverse cellulolytic microorganisms (esp. bacteria) are harbored in the first of these chambers (the forestomach). Caeco-colic fermenters are those animals that have an enlarged cecum or colon as the primary fermentation chamber. Enlarged caeco-colic regions in primates are common and found in some species of prosimians, platyrrhines, cercopithecines, and hominoids. Cercopithecines and hominoids in particular have well-developed colons (Hill 1958; Milton 1993; Lambert 1998).

Plant cell walls require considerable fermentation before they are useful as an energy source, and longer digestive retention times result in more fermentation (Milton 1981, 1984, 1986, 1993; Lambert 1998; Remis 2000; Lambert and Fellner 2012). It is typically argued that "both the total capacity of the digestive tract and the capacity available for microbial fermentation are almost directly proportional to body mass" and that only an increase in body size would allow longer retention times (Cork and Foley 1991, p. 139; Kay and Davies 1994). As such, it has historically been assumed that smaller primates will have (both absolutely and relatively) faster food passage rates than larger species, thereby limiting their capacity to ferment fibrous plant components (Parra 1978; Kay 1985; Cork and Foley 1991; Kay and Davies 1994; Van Soest 1996).

Yet, both cercopithecoid subfamilies have relatively longer digestive retention times than the much larger African apes (Lambert 2002c; Blaine and Lambert 2012). This is not unexpected among the Colobinae; on average, their mean digestive retention times range from roughly 40 to 60 h (Lambert 1998; Caton 1999). Neither cercopithecines nor hominoids exhibit such derived anatomy, their simple-stomached gastrointestinal anatomy is very similar. Yet, in an analysis regressing digestive retention times as a function of body size, Lambert (1998) found that the cercopithecines in the analysis were significantly further above the regression line than any other primate taxon. A more recent analysis, including more species (Blaine and Lambert 2012), corroborated this pattern. Indeed, despite being on average an order of magnitude smaller than African apes, all tested cercopithecines exhibit mean digestive retention times averaging 31 h (*P. troglodytes*, 31.5–48 h; *G. gorilla*, 36.5–61.9 h (Lambert 1998, 2002c; Milton and Demment 1988; Remis 2000)). These digestive results have important implications for understanding how monkeys can consume either similar or greater levels of fiber than larger-bodied apes (Lambert 2002c; Blaine and Lambert 2012).

Chemical Defenses and Detoxification

There are two primary mechanisms for detoxifying plant toxins: (1) microbial activity in a specialized stomach and (2) microsomal enzymes (Freeland and Janzen 1974).

Colobines rely on their microbial community in their derived stomach, while cercopithecines and apes must rely on microsomal enzymes. While we know extremely little about such microbial mechanisms in colobines, the potential of the specialized stomach with a diverse and dense microbial community to act as a detoxification chamber has been demonstrated in ruminating ungulates (Keeler et al. 1978; Waterman and Kool 1994).

Mammals without the advantage of forestomach microbial activity rely heavily on microsomal enzymes to detoxify plant toxins (Freeland and Janzen 1974). Microsomal enzymes are located in the endoplasmic reticula of hepatocytes and are activated in the presence of toxins, usually after digesta has left the stomach and entered the intestines. All noncolobine primates rely on this system.

Being smaller in body size can be advantageous for enzyme production since rates of enzymatic activity scale negatively with mammal body size (Walker 1978; Freeland 1991). Freeland (1991) thus suggests that smaller mammals are at an advantage for detoxifying plant secondary metabolites and that the larger the mammal, the greater the preference for foods with low amounts of toxic plant metabolites. These assertions rest largely on results by Walker (1978) who has expressed rates of enzyme activity in rats as a function of liver mass relative to body mass. On average, cercopithecines are smaller than colobines and apes, which may facilitate their consumption of chemically defended plants not available to apes and only available to colobines as a consequence of their specialized stomachs.

Accordingly, relative to apes, cercopithecoids are at an advantage in their capacity to deal with fiber and plant defenses. Colobines thoroughly digest their high-fiber foods via a specialized stomach and tolerate potentially high levels of plant toxins via a diverse microbial community in this stomach. Cercopithecines, on the other hand, have a simple stomach and instead extract nutrients out of the diet via extensive digestive retention. By staying small relative to apes, cercopithecines are able to maintain high levels of enzyme production for dealing with toxins. Incidentally, staying small also keeps absolute requirements for food low and also facilitates a faster life history strategy with higher reproductive output than apes. African apes, too, have a simple stomach, but have the digestive retention times expected for their body mass (Milton and Demment 1988; Lambert 1997, 2002c; Remis 2000). These larger-bodied primates avoid exposure to toxins and maintain higher-quality dietary components throughout the year, regardless of their scarcity; in the case of chimpanzees, this is facilitated by tool use. Like other African apes, early hominins probably also generally avoided toxins and high fiber, but eventually evolved myriad cultural adaptations for breaking down fiber and toxins, including soaking and cooking foods (Aiello and Wheeler 1995; Johns 1996; Milton 1999; Wrangham et al. 1999; Wrangham 2009).

Ecological and Evolutionary Implications

These digestive and feeding adaptations have implications for interpreting extant and extinct patterns of African monkey and ape species diversity (including both abundance and richness). Cercopithecidae is the most successful extant primate taxon and is so in all ways in which evolutionary and ecological success is defined: speciosity, abundance, and distribution. Indeed, despite being the youngest of all primate lineages, Cercopithecidae comprises more taxa than any other extant primate family and exhibits rates of cladogenesis approximately double that of all other primate taxa (Purvis et al. 1995). Moreover, cercopithecid taxocenes achieve the highest abundance of all extant primate communities (Fleagle 2013; Janson and Chapman 1999). In addition, Cercopithecidae is the most geographically widespread of all primate families and has successfully colonized habitats spanning the full spectrum of seasonality and food resource availability and distribution (Richard et al. 1989; Jolly and Whitehead 2000; Jablonski 2002).

Remaining fairly small keeps cercopithecoid absolute requirements for foods low relative to apes. Moreover, the carrying capacity for monkeys in a given habitat is essentially higher: a function of the fact that more items are food for cercopithecoids. These two factors may account for striking differences in monkey and ape density and biomass in Africa. For example, cercopithecoid density in Kibale National Park, Uganda, is 420 kg/km^2, while chimpanzee density is 3 kg/km^2; the biomass differences are 2,611 and 85 kg/km^2, respectively (Chapman and Lambert 2000). This pattern holds elsewhere in Africa. In Tai Forest, for example, the cercopithecoid biomass compared to that of chimpanzees is 951.7 versus 58.3 kg/km^2 (Chapman et al. 1999). In Budongo, Uganda, the biomass of cercopithecines is 354 kg/km^2 and chimpanzees 89 kg/km^2, and in the Lope Reserve, Gabon, where both *P. troglodytes* and *G. gorilla* are found, the monkey biomass is 251.4 kg/km^2, and ape biomass is 65.8 kg/km^2 (Plumptre and Reynolds 1995; Chapman et al. 1999).

Extant cercopithecoids are also greatly more speciose than apes. As has been noted by a number of authors, this pattern of diversity is a relatively recent one and has changed dramatically since the Miocene. During that epoch (23–5 Myr), hominoid species richness was at its maximum. In their species diversity and range of ecological adaptations and body sizes, Miocene apes paralleled the diversity of modern Cercopithecoidea (Andrews 1981; Kelley 1992). Since the Miocene, however, hominoid species diversity has steadily decreased, from a maximum of four to six sympatric species in the earlier millennia of the epoch to no more than two species living in a single habitat in the later Miocene and present (Andrews 1981). Conversely, while cercopithecoid diversity was relatively low in the Early Miocene, it has increased steadily, eventually achieving levels comparable to extant patterns (Purvis et al. 1995).

Several explanations have been proposed to account for this shift in hominoid-cercopithecoid diversity (Napier 1970; Ripley 1979; Andrews 1981; Temerin and Cant 1983). Each explanation is based on the concomitant assumptions that there was competition for increasingly scarce food resources between Miocene monkeys and apes and that this competition resulted in an ape adaptive pattern and a monkey adaptive pattern for foraging and feeding. Early African monkeys and apes are viewed to have been in competition for increasingly scarce fruiting resources during a time of extensive environmental change (cooler, dryer) in Miocene Africa

(Andrews and Van Couvering 1975). Napier (1970) argued that, in the face of increasingly patchy fruit availability in a changing East African habitat, the divergence of the cercopithecoids was directly related to their ability, via specialized bilophodont molars, to consume leaves. Similarly, Ripley (1979) argues that increasing East African forest seasonality played an important role in Old World monkey/ape divergence, although rather than on the dentition, she places emphasis on locomotor differences. Andrews (1981) refined Napier's (1970) hypothesis on cercopithecoid-hominoid divergence and suggested that monkeys diverged from apes as a result of their being able to exploit unripe fruits. Like Napier's scheme, his support stems largely from dental evidence.

Temerin and Cant (1983) proposed a model of ecological energetics to explain the differences in monkeys and apes. In this scheme, the authors argue that "when consuming the same category of food items (ripe fruit, leaf shoots, young leaves, etc.) apes exploit more widely distributed and/or smaller patches on average than do OWM" (Temerin and Cant 1983, p. 343). Their fundamental premise is that in the same environment, with access to the same resources, monkeys emphasize energy gain, while apes decrease energy expenditure because of their more efficient, specialized locomotion. They argue that in a habitat with increasingly rare fruit resources, Miocene monkeys did not move greater distances to maintain a heavily frugivorous diet; rather, they shifted to other food types. Conversely, apes did not shift their dietary proportions, but instead traveled longer distances to exploit increasingly rare fruit; this was facilitated by their specialized postcrania and efficient locomotion.

Several predictions have been made regarding Old World monkey and ape ecological distinctions and the shift in hominoid-cercopithecoid diversity from the Miocene to the present (Napier 1970; Ripley 1979; Andrews 1981; Temerin and Cant 1983). For example, Temerin and Cant (1983) predicted that, in a given environment, monkeys will eat more leaves and unripe fruit than apes and that monkeys will have higher assimilation efficiencies than apes on diets containing plant fiber. Similarly, Andrews (1981, p. 49) has argued:

> a critical distinction between apes and monkeys is the greater tolerance of the latter for a variety of plant secondary compounds, including tannins and alkaloids. Conversely, hominoid species avoid food with high levels of toxicity, and in particular they avoid unripe fruit that is eaten by monkeys. In developing a tolerance for tannins and other secondary compounds, therefore, the cercopithecines are able to tolerate less ripe fruit than the hominoids and thus gain access to fruiting trees before the hominoids.

These predictions have been borne out in the subsequent decades of primate field research. Yet, to date, there have been no explicit hypotheses regarding what these "assimilation efficiencies" and "tolerances" are or how they work. I suggest that they are specialized features of digestive and detoxification systems, including either long retention times/relatively high rates of microsomal enzyme production in the case of cercopithecines (in addition to amylase producing cheek pouches; Lambert 2005) or specialized stomach and microbial action in the case of the colobines.

On the basis of the variation in shearing quotients (SQ) in fossil apes, Ungar and Kay (1995) argue that the dietary breadth of Miocene hominoids was much greater than it is today, with fossil ape species occupying a variety of trophic niches, including folivory, soft-object frugivory, and hard-object feeding (seeds). That Miocene apes ranged in size from the small *Micropithecus clarki* at 3.5 kg to *Afropithecus* and *Proconsul major* weighing in at about 50 kg (Fleagle 2013) has been used in support of arguments regarding dietary range in Miocene apes. However, my proposition deflates the theoretical importance of body mass in driving the Miocene monkey/ape divergence. While it is commonly held that large-bodied primates have a greater capacity for fermentation and longer retention times (Gaulin 1979; Fleagle 2013), it appears that, in fact, cercopithecines successfully evolved this capacity without necessarily evolving large body size. Smaller mammals do have relatively greater metabolic needs than larger ones. However, rather than requiring a high-quality diet that is digested and processed quickly in order to maintain a high rate of incoming food, cercopithecines simply make *more* out of a lower-quality diet via detoxification and fermentation. Indeed, I suggest that from a dietary perspective, smaller, "monkey-sized" apes of the Early Miocene were not necessarily analogs of later similarly sized monkeys. Although Miocene apes may have had the dental features correlated with folivory and seed eating (i.e., high SQ), they may have ultimately been outcompeted by cercopithecoids, because monkeys had both dietary *and* digestive features that enabled them to deal with a broader diet (i.e., colobines had a sacculated stomach and microbial detoxification, and cercopithecines long retention times, high rates of enzyme production, and cheek pouches) and were simply *better* at extracting nutrients/resources out of a variety of food types (Lambert 2005). Thus, cercopithecoids of the Miocene and thereafter were better equipped to deal with the variety of niches originally occupied by the dental apes. Apes of the Middle to Late Miocene may have been essentially outcompeted (digestively) in these other niches and, as a result, became better frugivores, resulting in the highly selective fruit-feeding behavior we see today.

Conclusion

In short, I suggest that at some point early in their radiation, cercopithecines increased the breadth of their dietary niche and did so by remaining small and evolving digestive adaptations in the form of long retention times and cheek pouches (Lambert 2005). As the cercopithecoids diverged, colobines took off on a different evolutionary trajectory and opted for a previously unfilled primate dietary niche (specialized arboreal folivore) by evolving a specialized stomach. Relative to apes, cercopithecoids have a faster life history strategy (see chapter "▶ Primate Life Histories," Vol. 2), with much greater reproductive output; a consequence of this is that these smaller primates tend to evolve more quickly, which may explain their greater speciosity (Cowlishaw and Dunbar 2000). Hominoids opted for a specialized strategy and are essentially "trophically restricted" (sensu Ungar and Kay 1995) relative to the smaller cercopithecoids, while hominins pursued a trajectory of increasing dietary quality both by increasingly including vertebrate meat into the diet and by cultural adaptations such as cooking (Milton 1999; Wrangham et al. 1999; Wrangham 2009; Stanford and Bunn 2001).

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The Hunting Behavior and Carnivory of Wild Chimpanzees

Nicholas E. Newton-Fisher

Contents

Abstract

The pursuit, capture, and consumption of small- and medium-sized vertebrates appear to be typical of all chimpanzee (*Pan troglodytes*) populations, although

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N.E. Newton-Fisher (✉)
School of Anthropology and Conservation, University of Kent, Canterbury, Kent, UK
e-mail: n.e.newton-fisher@kent.ac.uk

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large variation exists. Red colobus monkeys (*Piliocolobus* sp.) appear to be the preferred prey, but intensity and frequency of hunting vary from month to month and among populations. Hunting is a predominately male activity and is typically opportunistic, although there is some evidence of searching for prey. The degree of cooperation during hunting, as well as prey selection, varies between East and West African populations and may be related to the way the kill is divided: in West Africa, hunters often collaborate, with kills tending to be shared according to participation, whereas in East Africa, cooperation in hunting is more limited, and the kill is typically consumed selfishly or divided in response to harassment (begging) by others. In some cases, it may be shared tactically, trading meat with other males to strengthen alliances. The adaptive function of chimpanzee hunting is not well understood, and a variety of hypotheses have been proposed. Ideas that chimpanzees hunt to make up for nutritional shortfalls, or to acquire meat to trade for sex, have failed to find empirical support, while recent work favors nutritional benefits of some kind. Nevertheless, cross-population studies evaluating multiple hypotheses are in their infancy, and there is much to be learned. In particular, very little is known about hunting of nonprimates, particularly ungulates, or the impact that variation in levels of hunting, and of carcasses to share and consume, has on patterns of chimpanzee behavior. If one goal of studying this topic is to shed light on the behavioral ecology of hominins, then efforts to understand the diversity of hunting and carnivory in wild chimpanzees are needed.

Introduction

Hunting – the pursuit, capture, and consumption of small- and medium-sized vertebrates – appears to be typical of all chimpanzee (*Pan troglodytes*) populations. Such behavior has aroused considerable interest among anthropologists since it was first reported (Goodall 1963). Hunting, the division of the kill, and the consumption of meat all play an important role in the lives of modern hunter-gatherer societies (Lee 1979; Kaplan and Hill 1985; Hawkes et al. 2001; Hawkes and Bird 2002) and factor in a number of hypotheses concerning human evolution (Washburn and Lancaster 1968; Isaac 1978; Hill 1982; Tooby and DeVore 1987; Stanford 1996, 1998, 2001). While early ideas such as "Man the Hunter" (Washburn and Lancaster 1968) have been largely discredited, hunting as a means to acquire meat remains important in many modern scenarios (Domínguez-Rodrigo 2002; Hawkes and Bird 2002). Animal tissue has high calorific value relative to plant material, is rich in fat and protein, and contains essential amino acids (Milton 1999). It is therefore a valuable resource. The nonrandom sharing of meat has been proposed as an important selective force driving the evolution of intelligence (Stanford 2001), and the consumption of meat has been invoked as an important proximate factor enabling the evolution of larger brains in the *Homo* lineage (Aiello and Wheeler 1995).

Chimpanzees show large variation between populations in the choice of prey species, frequency of hunting, and the techniques employed. Understanding both how and why chimpanzees hunt is important for the framing of evolutionary hypotheses; chimpanzees provide our best evidence for the behavioral capabilities of early hominins (Domínguez-Rodrigo 2002). In this chapter, substantially revised and updated from the previous version (Newton-Fisher 2007), I review the data concerning hunting behavior among wild chimpanzees and address current hypotheses concerning the reasons why chimpanzees hunt, drawing out both similarities and differences between populations in their hunting behavior.

Characteristics of Chimpanzee Hunting

All known populations of chimpanzees show some evidence of hunting and consuming vertebrate prey. Such hunting has been documented systematically among the East African chimpanzees (*Pan troglodytes schweinfurthii*) of the Gombe (van Lawick-Goodall 1968; Teleki 1973; Busse 1977; Stanford 1998; Gilby 2006; Gilby et al. 2006, 2010) and Mahale (Nishida et al. 1979; Takahata et al. 1984; Uehara 1997) National Parks in Tanzania and of the Kibale Forest National Park (Mitani and Watts 1999; Watts and Mitani 2002; Teelen 2008; Gilby et al. 2008; Watts and Amsler 2013) in Uganda, as well as among the West African chimpanzees (*P. t. verus*) of the Taï National Park, Cote d'Ivoire (Boesch and Boesch 1989; Boesch and Boesch-Achermann 2000; Gomes and Boesch 2009). Other reports of hunting by chimpanzees come from East African populations in the Budongo Forest, Uganda (Newton-Fisher et al. 2002), Kahuzi-Biega National Park, DRC (Basabose and Yamagiwa 1997), Kasakati, Tanzania (Kawabe 1966), and Semliki, Uganda (Hunt and McGrew 2002); from central African populations (*P. t. troglodytes*) of Lopé, Gabon (Tutin and Fernandez 1993) and Ndoki, Cameroon (Kuroda et al. 1996; Takenoshita 1996); from the Ebo forest, Cameroon (*P. t. ellioti*) (Morgan et al. 2013); and from West African populations of Mt. Assirik, Senegal (McGrew 1983; Hunt and McGrew 2002), Bossou, Guinea-Bissau (Sugiyama and Koman 1987), and Tenkere, Sierra Leone (Alp and Kitchener 1993).

Prey Diversity

Across populations, prey diversity is high with at least 40 species of vertebrates targeted. Chimpanzees show a clear focus on mammalian prey (Table 1) and are known to consume a variety of primate species as well as ungulates and rodents but will also eat birds, lizards, and frogs. Some populations have a diverse range of prey, whereas others are more specialized. The Mahale chimpanzees, for instance, are known to hunt at least 17 species of mammals, while in Taï, chimpanzees hunt only 7 (all primates) of the 15 sympatric mammal species (Boesch and Boesch-Achermann 2000; Boesch et al. 2002). Prey are typically small, up to a maximum of

Table 1 Diversity of mammalian prey hunted by chimpanzees across Africa

	Pan troglodytes schweinfurthii							*P. t. troglodytes*		*P. t. verus*			
	Budongo	Gombe	Kahuzi	Kasakati	Ngogo	Mahale	Semliki	Lope	Ndoki	Assirik	Bossou	Taï	Tenkere
Primates													
Red colobus													
Piliocolobus badius												✓	
Piliocolobus tephrosceles		✓			✓	✓							
Black and white colobus													
Colobus guereza	✓				✓		✓						
Colobus polykomos												✓	✓
Colobus satanas								✓					
Olive colobus													
Procolobus verus												✓	
Gray-cheeked mangabey													
Lophocebus albigena					✓			✓					
Sooty mangabey													
Cercocebus atys												✓	
Olive baboon													
Papio anubis		✓			✓								

Yellow baboon													
Papio cynocephalus						✓							
Vervet monkey													
Chlorocebus pygerythrus						✓							
Red-tailed monkey													
Cercopithecus ascanius	✓	✓		✓	✓								
Campbell's monkey													
Cercopithecus campelli													✓
Diana monkey													
Cercopithecus diana												✓	
L'Hoest's monkey													
Cercopithecus l'hoesti			✓		✓								
Blue monkey													
Cercopithecus mitis	✓	✓	✓		✓	✓							
Mona monkey													
Cercopithecus mona											✓		
Lesser spot-nosed monkey													
Cercopithecus petaurista											✓		

(*continued*)

Table 1 (continued)

	Pan troglodytes schweinfurthii							*P. t. troglodytes*		*P. t. verus*			
	Budongo	Gombe	Kahuzi	Kasakati	Ngogo	Mahale	Semliki	Lope	Ndoki	Assirik	Bossou	Taï	Tenkere
Crowned monkey													
Cercopithecus pogonias									✓				
Bushbaby													
Galago sp.						✓							
Potto													
Perodicticus potto											✓		
Chimpanzee													
Pan troglodytes	✓	✓			✓	✓							
Ungulates													
Forest duiker													
Cephalophus sp.	✓				✓				✓			✓	
Blue duiker													
Cephalophus monticola	✓				✓	✓		✓					
Bushbuck													
Tragelaphus scriptus		✓				✓							
Bushpig													
Potamochoerus porcus		✓				✓							

Warthog													
Phacochoerus aethiopicus						✓							
Others													
Giant elephant shrew													
Rhynchocyon sp.						✓							
Yellow-spotted hyrax						✓							
Heterohyrax brucei													
White-tailed mongoose													
Ichneumia albicauda						✓							
Civet													
Civettictis civetta						✓							
Rodents (various spp.)		✓	✓			✓			✓		✓	✓	
Pangolin									✓	✓			

Populations (study sites) of chimpanzees are arranged by subspecies. A ✓ indicates that the species has been recorded being killed or consumed. Not all species of prey are present at all sites around 20 kg – the weight of an adult male black and white colobus monkey (*Colobus guereza*) (Kingdon 1997) or a part-grown bushpig (*Potamochoerus porcus*) – but often much smaller (Goodall 1986).

Prey Specialization

Monkeys, in particular colobus monkeys, appear to be the main prey of chimpanzees wherever the species are sympatric. Red colobus (*Piliocolobus tephrosceles* in East Africa, *Piliocolobus badius* in West Africa) are the primary prey for many populations of chimpanzees, with black and white colobus (*Colobus guereza* in East Africa, *Colobus polykomos* in West Africa) as a secondary target.

The degree to which chimpanzees specialize on monkeys to the exclusion of other prey species varies between populations. In the Taï Forest, chimpanzees show a notably strong specialization. Between 1984 and 1995, 249 of 267 known kills were of colobus monkeys: 80.5 % red colobus (*Piliocolobus badius*) and 12.7 % black and white colobus (*Colobus polykomos*) (Boesch and Boesch-Achermann 2000). A similar specialization is apparent among the Ngogo chimpanzees of the Kibale forest, where between 1995 and 2000, 92.5 % of all prey were colobus monkeys: 87.8 % red colobus (*Piliocolobus tephrosceles*) and 4.7 % black and white colobus (*Colobus guereza*). At Gombe, the specialization is less extreme but still noticeable: red colobus (there are no black and white colobus at this site) constituted 59 % of the chimpanzees' prey between 1970 and 1975, 66 % between 1976 and 1981, and 84.5 % between 1990 and 1995 (Goodall 1986; Stanford 1998).

By contrast, red colobus constituted only 53 % of all prey for the Mahale chimpanzees (Nishida et al. 1992), while black and white colobus (*Colobus guereza*) were 43.8 % of all prey for the Sonso chimpanzees of the Budongo Forest, where there are no red colobus (Newton-Fisher et al. 2002). These two populations appear to differ from the others in that the chimpanzees also prey upon small ungulates, particularly blue duiker (*Cephalophus monticola*), to an appreciable degree: 34 % of all prey in Mahale (Nishida et al. 1992) and 25 % of all prey in Budongo (Newton-Fisher et al. 2002). Data from Budongo are sparse, but observations support the idea that these chimpanzees do not demonstrate the extreme prey specialization seen in Taï and Ngogo (Newton-Fisher unpublished data). Forest ungulates, particularly duiker and bushpig, are in fact hunted by all the East African chimpanzee populations that have been studied (Gombe: Goodall 1986; Mahale: Nishida et al. 1992; Budongo: Newton-Fisher et al. 2002; Kibale: H. Sherrow personal communication) but do not appear to be regarded as prey by West African chimpanzees (Uehara 1997; Boesch and Boesch-Achermann 2000). More research is needed regarding chimpanzee predation on ungulates.

Chimpanzee populations also appear to differ in their choice of the age and sex of prey. For the Taï chimpanzees, half of their colobus monkey prey are adult, mostly females (Boesch and Boesch-Achermann 2000). This is in contrast to chimpanzees at Mahale and Gombe, where the vast majority of colobus prey are juveniles and infants (Goodall 1986; Uehara 1997) and some chimpanzee hunters target very young colobus monkeys, snatching them from their mothers (Stanford 1998). Somewhere between 75 % (Stanford et al. 1994) and 86 % (Stanford 1998) of red colobus prey at Gombe are immature individuals. For the Ngogo (Kibale) chimpanzee, the figure is somewhat less: 53–75 % (Mitani and Watts 1999; Watts and Mitani 2002). There is less information on the age and sex of non-colobus prey. Among the ungulates, bushbucks are targeted only as infants (fawns), as typically are bushpig (piglets) (Goodall 1986). Age and sex estimates of duiker kills are more difficult to obtain, given that the prey is rapidly torn apart and consumed entirely by the chimpanzees; however, it is clear that chimpanzees are quite capable of killing adult blue duiker (personal observations).

Sex Bias in Hunting

The hunting of monkeys is a predominately male activity. Among the chimpanzees of the Ngogo (Kibale) community, adult or adolescent males made 98.8 % of all kills recorded between 1995 and 2000 (Watts and Mitani 2002). In two decades of data from Gombe, adult males were responsible for 91.5 % of all kills (Stanford 1998). Female chimpanzees will and do hunt, however. Data from Gombe for 1977–1979 showed that females joined an average of 26 % (median: 25 %, range: 0–67 %) of red colobus hunts for which they were present and those females who were more likely to join males in a hunt were also more likely to hunt when apart from the males (Goodall 1986). One female, Gigi, contributed 4 % of the total kills (Stanford 1998). Any kills that females made as part of mixed-sex hunting party were likely to be taken by males (Goodall 1986), however, which may in part explain female unwillingness to hunt when males are present. Females may prey more on ungulates (Uehara 1997), but quantitative data are difficult to collect, in part due to the nature of ungulate hunting. The hunting of lesser bushbabies (*Galago senegalensis*) in Fongoli, Senegal, is rather different to the typical group hunts of monkeys: it is tool assisted, extractive, and individualistic; it also shows a strong female bias, with 14 of 22 observations of female hunters and only one of an adult male hunting in this way (Pruetz and Bertolani 2007).

Hunting Frequency

Detecting hunting in a chimpanzee population can be problematic, particularly if the chimpanzees are poorly habituated to human observers. Typically in this situation, hunting is rarely if ever seen, and studies rely on finding animal remains such as skin or bone in chimpanzee feces (McGrew 1992). Unfortunately, feces do not appear to provide a reliable indicator of hunting: while the presence of remains can confirm that consumption does occur, little can be said about its frequency (cf. Uehara 1997). For example, long-term observations of habituated chimpanzees in the Taï Forest have revealed a pattern of frequent hunting and consumption that is not mirrored in the pattern of prey remains found in fecal samples (Boesch and

Boesch-Achermann 2000). Further, fecal sampling can say nothing about the number of hunting attempts that fail to secure prey, the division of the prey once obtained, or the relative importance of scavenging as a method of acquiring meat. Similar problems may also occur when hunting is actually rare or when prey species are alerted or scared away by the presence of humans accompanying the chimpanzees, although in some cases chimpanzees may exploit their prey's fear of humans to increase hunting success (Goodall 1986; Boesch 1994).

Predation Pressure

While in some populations chimpanzees hunt only rarely, in others they are significant predators who hunt at levels that appear to be unsustainable (Goodall 1986; Wrangham and van Zinnicq Bergmann Riss 1990; Teelen 2008; Watts and Amsler 2013). Estimates for Gombe suggest that anything from 8 % to 42 % of the colobus population can be killed annually, with this proportion varying from year to year, 8–13 % (1973–1974: Busse 1977), 41.6 % (1972–1975: Wrangham and van Zinnicq Bergmann Riss 1990), and 16.8–32.9 % (1982–1991: Stanford et al. 1994), while at Taï during the 1980s, the figure was between 3 % and 8 % (Boesch and Boesch-Achermann 2000). For Ngogo, Teelen (2008) estimated 15–53 % of the red colobus population is killed by chimpanzees annually, while Watts and Amsler (2013) estimated that almost 2,500 red colobus monkeys were killed in the period 1998–2012, an average of 20.4–24.8 % of the population per year. By contrast, the Mahale chimpanzees were estimated to kill only around 1 % of the red colobus population each year during the 1980s (Boesch et al. 2002). Basabose and Yamagiwa (1997) estimate that the chimpanzees of Kahuzi-Biega kill 11–18 % of the *Cercopithecus* monkey population each year (predominately *Cercopithecus mitis* but also *Cercopithecus l'hoesti*). Hunting of ungulates may also impose high levels of mortality. Wrangham and van Zinnicq Bergmann Riss (1990) estimated chimpanzee-imposed mortality on bushbuck at 27 % (although this figure includes bushbuck fawns killed by baboons and subsequently stolen by chimpanzees) and on bushpig at 7 %, for populations in the Gombe National Park between 1972 and 1975.

These estimates, both for primates and ungulates, are based on comparing the number of kills with the population density of prey within the chimpanzee community's home range. There is potential for error in the estimates of each of these variables. If, for example, home range is overestimated (cf. Newton-Fisher 2004), then predation pressure will be underestimated, while underestimating the number of potential prey will inflate the estimate of predation pressure (Wrangham and van Zinnicq Bergmann Riss 1990).

Nevertheless, the level of predation by some chimpanzee communities on red colobus monkeys is extreme. As a reference point, predation by crowned eagles on the total cercopithecoid monkey population at Ngogo is estimated at 2 %: Mitani et al. (2001). There is good evidence that a significant decline in red colobus monkeys in the Ngogo region of the Kibale forest, at least since the mid- to late

1990s and possibly since the 1970s, is the result of chimpanzee predation (Teelen 2008; Lwanga et al. 2011; Watts and Amsler 2013). Simulations using 3 years (2001–2003) of Ngogo data showed that chimpanzee predation was likely to drive the red colobus population to local extinction within two decades without a dramatic change in the level, or success, of chimpanzee hunting (Teelen 2008). Local extinction is more probable if neighboring communities of chimpanzees also impose significant predation pressure (Watts and Amsler 2013) as this removes any "source" population from which immigrants can be drawn (*contra* Lwanga et al. 2011). The decline in red colobus in Ngogo has, however, been accompanied by a decline in chimpanzee hunting (encounters, hunts, and prey offtake) which appears to be a consequence of the reduced availability of prey: when these chimpanzees expanded their territory in 2009 (Mitani et al. 2010), they increased rates of both prey encounters and hunting (Watts and Amsler 2013).

Variation in Hunting Frequency

Estimates of hunting frequency and predation pressure typically disguise wide variation. Within a single community, the total number of hunts can vary from month to month and year to year. Across populations, chimpanzees appear to have hunting "seasons" during which the number of kills increases as a result of either more hunting, more successful hunting, or both. For the chimpanzees at Gombe, Mahale, and Taï, this hunting season falls toward the end of the year, peaking in September and October. At Gombe, this corresponds to the later part of the dry season (Stanford 1998; Gilby 2004). At Mahale, the peak is slightly later, reaching into November, and appears to coincide with the end of the dry season and the first rains of the wet season (Takahata et al. 1984). Preliminary work at Budongo suggested a dry season (December to February) peak in hunting activity (Newton-Fisher et al. 2002), but subsequent work has failed to confirm this idea (Newton-Fisher unpublished data).

The hunting behavior of the Ngogo chimpanzees does not appear to correspond to timing of rainfall, but hunting seasons instead occur during periods of fruit abundance (Watts and Mitani 2002) that are not correlated with rainfall (Mitani et al. 2002). Similarly, the hunting season at Mahale occurs when more fruit is available (Uehara 1997), and among the Kanyawara chimpanzees of the Kibale forest, hunting rates were higher when preferred species of ripe fruit were abundant (Gilby and Wrangham 2007). At Taï, the hunting season runs from mid-August to mid-November, between periods of low and high fruit abundance, and ends when chimpanzees switch to highly calorific *Coula edulis* nuts from which they gain sugar, protein, and fat. The peak in hunting is also in September and October, but this is during the wet season at the time of greatest rainfall (Boesch and Boesch-Achermann 2000).

In addition to these seasonal changes, hunting frequency within a single community varies between years, which may be related to changes in the abundance of prey species or the number of chimpanzees who might hunt. A comparison of hunting success for Mahale chimpanzees between the 1980s and early- to mid-1990s showed a threefold increase in the percentage of the red colobus population killed by the chimpanzees, rising from around 1 % to at least 3 % of the population per year (Boesch et al. 2002). This seemed to accompany an expansion in the red colobus population. Hunting success then fell in the later part of the 1990s, following a decrease in the number of chimpanzees in the study community (Boesch et al. 2002): a similar reduction in the level of hunting was seen following a decrease in the number of adult males in the study community in the Taï Forest (Boesch and Boesch-Achermann 2000).

Impact Hunters

Chimpanzees may also experience greater hunting success when individuals with a flair for hunting are present. These individuals ("impact" hunters) demonstrate both a high willingness to hunt and a consistently high probability of success (Goodall 1986; Stanford 1998; Boesch and Boesch-Achermann 2000). Typically, one or two males in each study populations where monkey hunting is prevalent have been identified as impact hunters (Goodall 1986; Stanford 1998; Boesch and Boesch-Achermann 2000; Gilby et al. 2008), with anecdotal evidence suggesting that these individuals are responsible for initiating hunts, climbing first toward prey. Other male chimpanzees may be spurred into hunting by the actions of these impact hunters. A recent increase in hunting of black and white colobus monkeys by Sonso (Budongo) chimpanzees has been ascribed to the actions of a particular male, while Stanford (1998) found that two males of the Kasekela (Gombe) community were highly successful when hunting alone and that one of these, Frodo, was both a catalyst for hunts and a fearsome predator of red colobus monkeys, killing at least 50 in the period 1990–1992. Gilby et al. (2008) tested the influence of impact hunters among the Kanyawara (Kibale) chimpanzees and found that the likelihood of a hunt occurring was much greater when an impact hunter was present, even when controlling for the number of adult males, and that the chance of other males joining a hunt increased if an impact hunter was hunting.

Hunting Binges

A further source of variation in hunting frequency within a community is the occurrence of hunting "crazes" (van Lawick-Goodall 1968) or "binges" (Stanford 1998). These are periods during which the chimpanzees hunt "almost daily": more than three hunts in a 7-day period, with chimpanzees appearing to hunt on contact with prey (Stanford 1998). In the Kasekela (Gombe) community, 23 binges were recorded between 1990 and 1995. The longest of these lasted 74 days and consisted of 38 observed hunts and at least 76 kills, all red colobus. Correcting the number of kills for observation time suggests that over 100 colobus monkeys were killed during this 74-day period (Stanford 1998). The Ngogo chimpanzees went on a 57-day hunting binge in 1998, during which they hunted 22 times, killing 69 red colobus, one mangabey (*Lophocebus albigena*), and one red duiker

(*Cephalophus* sp.). Only 4 of the 22 hunts were unsuccessful, including two attempts to hunt black and white colobus (*Colobus guereza*). This and other hunting binges at Ngogo coincided with major fruit crops, and most hunting occurred when large parties of males were traveling together (Watts and Mitani 2002). Large parties with high numbers of males also seem to be linked to hunting binges at Gombe (Stanford 1998). Large numbers of chimpanzees traveling together suggest that fruit is particularly abundant, and so hunting binges at Gombe may also be linked to periods of food abundance.

How Do Chimpanzees Hunt?

Many hunts are opportunistic, in that chimpanzees appear to decide to hunt after encountering prey during the course of normal foraging activities or travel around the home range. This seems to be the typical pattern at Gombe (Goodall 1986; Stanford 1998) and at Ngogo (Mitani and Watts 2001). Chimpanzees in Taï, however, show evidence of actively searching for prey, listing for the vocalizations of either colobus monkeys or Diana monkeys (*Cercopithecus diana*) with whom the colobus are frequently associated (Boesch 1994; Boesch and Boesch-Achermann 2000). The likelihood of a hunt when chimpanzees encounter potential prey varies: it is relatively high for the Kasekela (Gombe) community (40 %: Gilby et al. 2006) and the Ngogo (Kibale) community (37 %: Mitani and Watts 2001) but somewhat lower in the Kanyawara (Kibale) community (15 %: Wrangham, cited in Gilby et al. 2006).

Chimpanzees hunt the majority of their prey without the use of tools or weapons, although there are a few reports of rocks or branches being hurled, possibly in an attempt to panic defensive formations of adults (Goodall 1986), and tools (sticks and leaves) are sometimes used to aid in the processing of the carcass (McGrew 1992). In Fongoli, Senegal, chimpanzees fashion tools from branches, at times biting the end to create a point, which are forcibly jabbed into tree cavities: observations suggest that this is done to immobilize or kill lesser bushbabies (*Galago senegalensis*) that are then extracted and consumed (Pruetz and Bertolani 2007).

During a monkey hunt, prey are typically chased, seized, and then killed either by a bite, by disembowelment, or by being torn apart (Goodall 1986). Hunts may yield single or multiple kills (or, indeed, may fail completely). Between 1973 and 1981, Gombe chimpanzees made multiple kills in 37.5 % of colobus hunts; most of these were two kills per hunt. A typical colobus hunt at Gombe will produce two (Watts and Mitani 2002) or three (Stanford 1998) kills and at Ngogo, four kills (Mitani and Watts 2001). Single kills seem to be more usual for Taï chimpanzee hunters (Stanford 1998), although typically such kills are of adult monkeys (mean number of kills per successful hunt: 1.2: Watts and Mitani 2002). Failure rates (i.e., failure to kill any prey during a hunt) vary between communities. For the Tai and Gombe chimpanzees, around 50 % of hunts fail (Boesch and Boesch-Achermann 2000; Gilby et al. 2006), while for Ngogo chimpanzees the rate is lower, at 16 %

(Mitani and Watts 2001). In an analysis of hunting by chimpanzees of the Kanyawara community, Gilby et al. (2008) found that an individual hunter had around a 65 % chance of acquiring meat in any hunt that was successful; among the Taï chimpanzees, a male had access to meat in around 48 % of successful hunts (Boesch and Boesch-Achermann 2000).

Analysis of hunting data from both Ngogo (Watts and Mitani 2002) and Gombe (Wrangham 1975; Stanford et al. 1994; Gilby et al. 2010) indicates that hunting is responsive to habitat structure. At Ngogo, chimpanzees were more likely to hunt red colobus when encountering prey in, or close to, areas with broken or no tree canopy than when in primary forest (Watts and Mitani 2002); at Gombe, hunts were more likely and more successful in woodland and semi-deciduous forest than in evergreen forest. These observations suggest that, as with obligate predators, chimpanzees are more likely to hunt in areas where it is harder for prey to escape and hunting costs are lower (Gilby et al. 2010).

The hunting of ungulates is less well described. Bushpigs are probably the most difficult of ungulate prey. Chimpanzees are wary, if not fearful, of the adults, and they retreat to the trees in the face of aggression by adult pigs (personal observations). At Gombe, chimpanzees have been described using stealth to seize piglets before the adults are alerted to their presence and also of using aggressive displays to panic the adults, capturing piglets either in the confusion or if abandoned by adults that run off (Goodall 1986). Bushbuck fawns hide in dense cover as an antipredator strategy, while adults typically freeze or flee. Chimpanzees search for hiding fawns when their attention is drawn to particular areas by the presence of adult bushbuck or possibly auditory or olfactory cues. A captured fawn's mother may be aggressive toward chimpanzees, but this is difficult to determine as human presence causes them to flee (Goodall 1986). Duiker captures are typically opportunistic, with chimpanzees seizing them if they come within reach. Chimpanzees sometimes show interest in duiker vocalizations (personal observations), but the extent to which they search for duiker is unclear.

Cooperative Hunting?

Chimpanzees will hunt alone as well as in the company of others. Solitary hunts occur rarely at Taï (16 % of hunts: Boesch and Boesch-Achermann 2000) and Mahale (28 % of hunts: Takahata et al. 1984; Uehara et al. 1992), while they are more common at Gombe (64 % of hunts: Busse 1978; Teleki 1973) where the chimpanzees appear to be highly effective solo hunters. Boesch (1994) found that Gombe chimpanzees had a success rate of around 50 % when hunting alone, capturing an average of 2.46 kg of prey within 7 min of hunting. In contrast, his estimate for the success rate of lone hunters at Taï was only 13 %. The forest canopy is lower and more broken at Gombe than it is at Taï, which may make it easier for lone chimpanzees to isolate colobus monkeys and so allow them to capture and kill their prey more often and more quickly (Boesch 1994).

Group hunts are often a case of individual chimpanzees making their own efforts in a collective setting, perhaps exploiting the panic in the prey produced by the presence of multiple hunters, and reacting to the actions of other chimpanzees. Collaborative hunting, where males take particular roles such as “drivers” and “blockers” (Boesch and Boesch 1989), appears to be the primary form of hunting among the Taï chimpanzees (77 % of hunts: Boesch and Boesch-Achermann 2000) but is rare among the East African chimpanzees (Boesch 1994; Stanford 1998; Boesch and Boesch-Achermann 2000; Watts and Mitani 2002). A division of roles between those that pursue the prey and those that wait on the ground to capture monkeys that fall from the canopy is, however, fairly common among East African chimpanzees.

There is little consensus over the degree to which such collaborative hunting can be described as cooperative. To the extent that chimpanzees take different roles and are responsive to one another’s behavior during a hunt targeting monkeys, there is good evidence for social cooperation. To demonstrate that chimpanzee hunting is functionally cooperative, however, individuals need to do better when hunting as a group. Thus, if cooperation occurs, hunting attempts should be more successful when more individuals take part, or at least certain number of hunters should be more successful than solitary hunters. At Gombe, Ngogo, and Taï, the probability of killing prey during a red colobus hunt increases with the number of hunters present, but this appears to be a simple effect of more hands grabbing at the monkeys; there does not appear to be an additional effect from males working together (Stanford 1998; Gilby et al. 2006); at Kanyawara, however, there does appear to a synergistic effect (Gilby et al. 2008). Many chimpanzees, hunting together, may be able to overwhelm the defensive strategies of the red colobus and reduce the opportunities for panicked monkeys to escape. However, the mass of prey obtained per hunter does not correlate with the number of males hunting at Ngogo (Watts and Mitani 2002), and while Stanford (1998) found that Gombe chimpanzees gained a higher return (greater mass of prey per hunter) when more than seven are hunting together, Gilby et al. (2006), using a larger dataset from the same community, found that the mass of prey per hunter actually decreased with the number of adult male chimpanzees present. By contrast, among Taï chimpanzees the number of hunters is strongly correlated with the mass of prey caught because the likelihood of capturing an adult monkey increases, but gains per hunter peak at four males (Stanford 1998) presumably because most hunts terminate after the first kill.

Scavenging

Chimpanzees are reluctant scavengers: only a handful of reports describe such behavior. Most of these observations concern the seizing of fresh kills from other predators, a behavior often labeled “piracy” (Goodall 1986; Uehara 1997; Stanford 1998), although “plundering” – the forcible stealing of goods – might be more appropriate term. At Gombe, chimpanzees have been recorded plundering fresh kills from baboons (Morris and Goodall 1977; Goodall 1986), and at Budongo, the body of infant blue monkey (*Cercopithecus mitis*) was stolen from the adult blue monkey who killed it (Newton-Fisher et al. 2002). Boesch and Boesch-Achermann (2000) report three instances of Taï chimpanzees plundering red colobus captures from eagles while the monkeys were still alive and a further four instances of chimpanzees eating the kills of eagles: presumably these monkeys were freshly killed, although this information is not reported. Given that chimpanzees are quite willing, if they can steal or beg part of the carcass, to eat prey that chimpanzees other than themselves have killed, it is not surprising that they are similarly willing to take fresh kills from other species.

True scavenging – acquiring meat from an abandoned carcass – appears particularly rare, however. In 36 years of observation at Gombe, fewer than 20 instances were recorded (Stanford 1998), and at least nine of these (all red colobus) were likely, or known, to have been previous chimpanzee kills (Goodall 1986). Similar low rates have been recorded at Mahale, seven cases in over 25 years of observation: six ungulates and one red-tailed monkey (*Cercopithecus ascanius*) (Hasegawa et al. 1983; Uehara 1997). Scavenging has not been reported from Taï: Boesch and Boesch-Achermann (2000) record ten encounters with fresh carcasses, none of which were eaten by the chimpanzees.

Most encounters with fresh carcasses result in apparently curiosity-driven behaviors in the chimpanzees, with no indication that the chimpanzees regard these carcasses as a source of meat. Stanford (1998) reports an observation from Gombe of a juvenile male briefly chewing on 1- or 2-day-old colobus meat that was ignored by the adults, and Muller et al. (1995) record a further observation from the same community of a party of chimpanzees encountering a dead bushbuck, presumed to be killed by a leopard. The chimpanzees showed strong curiosity over the body, even grooming it, and one female rolled around inside the eviscerated carcass, but they did not feed (Muller et al. 1995). By contrast, chimpanzees at Mahale did feed on the carcasses of two adult bushbuck thought to be the remains of leopard kills (Hasegawa et al. 1983).

Meat Eating

All populations of chimpanzees subsist on a primarily frugivorous diet. Typically, fruit constitutes 60–80 % of the time spent feeding (Gombe: 63 %, Wrangham 1977; Kibale: 79 %, Wrangham et al. 1996; Budongo: 64.5 %, Newton-Fisher 1999a). This is supplemented by leaves, as well as other plant materials. Even in communities that hunt frequently, such behavior constitutes a very small portion of the time spent foraging. Watts and Mitani (2002) recorded 131 predation episodes in 6 years at Ngogo (1.8 hunts per month), while Boesch and Boesch-Achermann (2000) recorded 413 hunts in a 12-year period at Taï (2.9 hunts per month). Nevertheless, as discussed above, chimpanzees do hunt, kill, and consume meat, while competition over the division of the kill can be high.

The Value of Meat

Animal tissue, including muscle, internal organs, brain, and bone marrow, provides an easily digestible nutritious package (Stanford 1996; Milton 1999). Beyond any particular calorific value, it provides high-quality protein containing all essential amino acids, as well as long-chain polyunsaturated fatty acids, and a range of key micronutrients such as calcium, potassium, magnesium, zinc, B-group vitamins, and vitamin K. Commonly, chimpanzees consume the entire animal, including bones and skin, and will compete for the smallest scraps. A single carcass can, therefore, represent an important resource, despite variation in body size between prey species: adult *Colobus guereza* weigh up to 23 kg, although Ugandan populations may not reach this size, while the western black and white colobus (*Colobus polykomos*: adult male body weight of 8–12 kg) is smaller and similar in size to the eastern red colobus (*Piliocolobus tephrosceles*: adult male body weight of 13 kg); the western red colobus (*Piliocolobus badius*) are lighter, with an adult body weight of only 5–10 kg (Kingdon 1997); and blue duiker (*Cephalophus monticola*) can weigh up to around 9 kg, with duiker (*Cephalophus* sp.) meat providing 20.8 g/100 g of protein and 3.4 g/100 g of fat (Ntiamoa-Baidu (FAO) 1997).

The quantity of meat, including the associated elements of the carcass, that is consumed by some individuals may be relatively significant. In good hunting years, the total amount of meat consumed may be more than double that consumed in poorer years. The 45 chimpanzees of the Kasekela (Gombe) community in 1992 consumed over 500 kg of red colobus meat, and their total meat consumption for the year was probably close to 700 kg. The previous year (1991), colobus meat consumption was less than 200 kg, and in 1988, this figure was less than 150 kg (Stanford 1998). Averaged over years, the level of consumption in the 1980s and 1990s seems similar to the estimate of 441 kg of meat per year for the same community in the 1970s (Wrangham and van Zinnicq Bergmann Riss 1990; Stanford 1998).

Boesch and Boesch-Achermann (2000) estimated that, averaged across the year, male Taï chimpanzees consumed 186 g per day, while females consumed 25 g per day. Their estimates for Gombe chimpanzees, similarly averaged, were 55 g per day for males and 7 g per day for females. These are similar to estimates made by Stanford (1998) of 70 g per day for males during peak hunting season and by Wrangham (1975) of 22 g averaged over males and females. Gilby (2006) estimated that, for adult males of this community in 1999–2002, an individual in possession of a kill consumed between 0.25 and 2.5 kg (mean = 1.16 kg) of meat during each feeding bout. For the Taï chimpanzees between 1987 and 1991, males consumed a mean of 0.48 kg of meat per successful hunt, while females consumed a mean of 0.13 kg (Boesch and Boesch-Achermann 2000).

Thus, meat should be a valued resource for chimpanzees, although there are observations that question this conclusion. In particular, captured prey may be eaten only partly before being discarded. In the Taï Forest, adult cercopithecine monkeys have been treated in this way (Boesch and Boesch-Achermann 2000); at Gombe, chimpanzees have been observed discarding captured adult red colobus in favor of pursing immature monkeys (Boesch 1994; Stanford 1998) and giving a carcass to another individual in order to hunt again (Goodall 1986), while in the Budongo Forest, an adult male chimpanzee captured and killed an elephant shrew (*Rhynchocyon* sp.) but took only a single bite before discarding the carcass (Newton-Fisher unpublished data). Similarly, bodies of infant chimpanzees killed by adults are sometimes only partially eaten before being handed on to another individual or discarded completely (Newton-Fisher 1999b). Furthermore, any kills made during a group hunt are typically divided in some way among some or all of the chimpanzees present.

Begging and Food Sharing

Following a kill, there is commonly a degree of competition for the meat, the intensity of which reinforces the idea that chimpanzees desire and value this resource. If the chimpanzee in possession of the carcass has companions, these individuals will attempt to acquire part of the carcass. More dominant individuals may attempt to steal the entire carcass for themselves. Others will sit around the possessor and beg for a share of the meat. Begging individuals seem to exert a lot of pressure both by their presence and by their harassing gestures and vocalizations. Chimpanzees unwilling to share will commonly move away from the crowd of begging individuals, although they are likely to be followed. When harassed by one or two others, a chimpanzee may simply turn its back to prevent them reaching toward the carcass.

Sharing of prey can be either an active or passive process. Most sharing is passive and ranges from an individual patiently scrounging the scraps that fall from a carcass as the possessor feeds, through harassment of the owner of the carcass by gestures and vocalizations, to an individual who is not in possession of the kill taking a portion of carcass without the use of aggression. Active sharing is less common and involves the individual who possesses the carcass handing part, or all, of the carcass to another chimpanzee. There are a number of theories to explain why food should be shared and the patterns of sharing observed. These include tolerated theft, reciprocity, kin selection, mutualism, buy-off, and harassment. As they apply to chimpanzees, these theories have been discussed extensively elsewhere (de Waal 1989; Mitani and Watts 2001; Fruth and Hohmann 2002; Stevens 2004; Stevens and Gilby 2004; Gilby 2006).

Patterns of sharing appear to differ between West and East African chimpanzees. In the Taï Forest, West African chimpanzees tend to divide the kill among the individuals who participated in the hunt. Older and more dominant males gain a greater share of the meat, but hunters tend to receive more than nonhunters, even when socially subordinate. The amount of meat obtained by females is not dependent on participation in the hunt, but females will support hunters over nonhunters when there is competition (Boesch and Boesch-Achermann 2000). In East Africa, at Gombe (Stanford 1998), Mahale (Nishida and Hosaka 1996), Ngogo (Mitani and Watts 2001), and Budongo (Newton-Fisher unpublished data), chimpanzees use a different strategy for the division of the carcass: males tend to monopolize the carcass and share only with particular other adults, both male and female (although it is worth noting that while Gilby (2006) found that Kasekela (Gombe) males, particularly the alpha, controlled carcasses, these males only shared preferentially with adult females with whom they exchanged grooming and did not preferentially share with particular males).

The particular sharing strategy employed by West African chimpanzees may oblige them to hunt adult monkeys. Collaborative group hunting appears necessary to increase hunting success and to reduce the time spent hunting in a habitat that favors escape by the prey but may only work if males are rewarded for participating in the hunt (Stanford 1998). Colobus monkeys are smaller in West Africa than they are in East Africa, and this might make targeting juveniles unprofitable if the meat has to be shared among all hunters. For East African chimpanzees, the larger body size of the colobus monkeys may pose a greater hazard, and East African chimpanzees show greater fear of adult colobus monkeys than do those in West Africa. Adult colobus monkeys can successfully threaten and rout chimpanzees, chasing them from trees on occasion (Nishida et al. 1979; Goodall 1986; Boesch and Boesch 1989). Given that the strategy adopted by East African chimpanzees of targeting juvenile and infant chimpanzees appears to be profitable (Boesch 1994), the additional costs of targeting adult monkeys together with a less reliable, more individualistic approach to sharing may make hunting adult monkeys a less attractive option.

Why Do Chimpanzees Hunt?

This question, which addresses the adaptive value of hunting, remains to be answered. It is only recently that quantitative analyses comparing the various hypotheses have been undertaken (Mitani and Watts 2001; Gilby et al. 2006) and, while there are efforts to draw together results from different populations (Uehara 1997; Boesch et al. 2002), systematic analyses across populations are limited (Gilby et al. 2010). Chimpanzees are omnivores, and while those who eat meat, particularly in large quantities, should gain nutritional benefits, carnivory does not appear to be critical for survival or reproduction, and thus various hypotheses have been advanced to explain the existence of their hunting behavior.

Hunting for Nutrition

Early views of chimpanzee hunting favored the view that it was driven by nutritional demands. Teleki (1973) proposed that Gombe chimpanzees hunt to compensate for nutritional shortfalls, given the strong seasonality at this site. The body weights of Gombe chimpanzees are lower during the dry season (Williams et al. 2002), which may to be the consequence of low food availability, and hunting at Gombe is more pronounced during the dry season than it is during the wet season

(Stanford 1998; Gilby et al. 2006). A nutritional perspective was also emphasized by Wrangham (1975), with a similar view emerging from research at Mahale (Takahata et al. 1984).

Energy Shortfall

The particular hypothesis that chimpanzees switch to hunting to compensate for energy shortfalls finds little support: Gilby et al. (2006) found that once party size and number of swollen (i.e., likely to be ovulating and therefore sexually attractive) females were taken into account, there was no association between diet quality and hunting among the Gombe chimpanzees. Furthermore, Mitani and Watts (2001) and Gilby and Wrangham (2007) found that chimpanzees from the Kibale forest hunted more frequently as fruit became more abundant, suggesting that chimpanzees are more likely to hunt when they have enough surplus energy. This makes sense if hunting is energetically costly, and individuals risk not gaining enough meat following division of the kill to offset such costs.

Whether this relationship between food abundance and frequent hunting applies to all populations of chimpanzees remains to be determined, but, as discussed above, hunting seasons coincide with fruit abundance in Mahale (Takahata et al. 1984; Uehara 1997) although apparently not at Taï (Boesch and Boesch-Achermann 2000) where chimpanzees may gain shares of the kill that depend on their participation in hunting (Boesch 1994). If the Taï chimpanzees capture and kill a sufficiently large prey in each hunt and if they can rely on this system of dividing the meat, then net nutritional gains would accrue to all participants.

Meat Scraps

Boesch and Boesch-Achermann (2000) suggested that the nutritional value of meat beyond its calorific value might make even small amounts significant for chimpanzees. Gilby et al. (2008) and Tennie et al. (2009) formalized this idea as the “meat-scrap” hypothesis, which assumes that hunting functions as a means of acquiring micronutrients such as vitamins B_{12} and B_6 and the minerals iron and zinc which are important for primate health and present at relatively high levels in meat but at low levels or virtually absent from primate plant foods. By consuming small amounts of meat (“scraps”), chimpanzees gain these micronutrients without having to consume vast quantities of plant material. This hypothesis assumes a threshold, a minimum amount of meat necessary to accomplish this goal (Tennie et al. 2009).

Both Gilby et al. (2008) and Tennie et al. (2009) provide support for this hypothesis. Among the Kasekela (Gombe) chimpanzees, the probability of an individual acquiring some meat increased by 18 % with each additional hunter, while the total amount of meat per hunter was not correlated to the number of hunters (Tennie et al. 2009) and in fact declined when all adult males present were considered (Gilby et al. 2006). For chimpanzees of the Kanyawara (Kibale) community, males were also more likely to obtain meat as the number of hunters increased, although once there were five or more hunters, males could do as well by begging: accordingly, focal males were less likely to hunt when more than five other males were present (Gilby et al. 2008).

Hunting for Trade Goods

The nutritional content of meat and associated tissue, together with the fact that it is both divisible and portable, means that each portion has an inherent value and can be either consumed or given to another individual. Meat could therefore be considered to be a commodity that can be traded with other individuals for other goods or services, which for chimpanzees are likely to be biases in future social interactions such as support in agonistic confrontation or increased levels of grooming. Such a "biological markets" (Noë and Hammerstein 1995) perspective is implicit in two further hypotheses concerning chimpanzee hunting, both of which see an adaptation in the nonrandom sharing of kills. While the "meat-for-sex" and "male-social-bonding" hypotheses are commonly presented as alternatives (Mitani and Watts 2001; Watts and Mitani 2002), they could be considered to be different, context-dependent outcomes of the same social strategy. This "meat-as-commodity" hypothesis proposes that chimpanzees hunt to gain possession of a commodity (part or all of an animal carcass) which has economic value within chimpanzee society (Stanford 1998); they can then trade this to further whatever proximate goals are most pressing, providing meat to females in an effort to coerce their mating behavior or to allies when they have need of them.

Meat for Sex

The first of these trade-based hypotheses, labeled "meat for sex" by Mitani and Watts (2001), was proposed by Teleki (1973). He noted that cycling females with conspicuous anogenital swellings tended to receive meat from adult males more frequently than did females without these sexual swellings and suggested that males shared meat with females in exchange for sexual access. Swollen females are attractive to males (Dixson 1998) as the swellings generally indicate approaching ovulation, although females will also show swellings when pregnant (Wallis and Lemmon 1986). Supporting evidence for this hypotheses was provided by Stanford (1998) who found that, at Gombe, the presence of a swollen female in a party of chimpanzees was the best predictor of a hunt occurring when encountering a group of red colobus and reported five observations of females begging for meat from males and only being given part of the kill after copulating.

However, in detailed analyses of the Gombe data together with data from the Kanyawara community, Gilby et al. (2006, 2010) found no support for the "meat-for-sex" hypothesis: specifically, males did not preferentially share with potentially ovulating females, and males were not more likely to hunt when such females were present. Furthermore, very few copulations occurred in close temporal proximity to meat-sharing events (Gombe: 0.6 %; Kanyawara: 0.1 %: Gilby et al. 2010), and when sharing of meat did occur between a male and a swollen female, mating was equally likely before as after (Gilby et al. 2010). Parous females at Gombe were more successful than nulliparous females at obtaining meat from males, but this was the case whether swollen (72 % vs. 44 % of bouts) or not

(60 % vs. 30 % of bouts), and Kanyawara females showed a similar trend (Gilby et al. 2010). This is likely to be due to increased persistence or intensity of begging by parous females, rather than strategic sharing by males.

Similarly, at Ngogo, the presence of swollen females was not a significant predictor of hunting once the effect of the number of males was removed. Males of this community did preferentially share meat with swollen females but did not copulate with those females at a level above chance after sharing. Furthermore, they did not gain a larger share of matings if they did share with a female, comparing female cycles in which the male shared with those in which he did not (Watts and Mitani 2002). Among the Taï chimpanzees, Gomes and Boesch (2009) found no evidence of direct exchanges of meat for sex or of a relationship between meat sharing and mating frequency.

There are also theoretical reasons to question this particular hypothesis. Female chimpanzees show a highly promiscuous mating strategy (Nishida 1968; Sugiyama 1968), typically copulating hundreds of times with multiple males during a single ovulatory cycle (Wrangham 2002). As a result, it seems unlikely that they would require meat from males before mating; furthermore, males in possession of meat are typically high ranking: such males may be those most able to coerce female mating behavior through the use of aggression and so the least likely to need to trade anything with females in return for sex. For a more detailed discussion of this topic, see Gilby et al. (2010).

Male Social Bonding

The other theory that involves using prey as a trade good is the “male-social-bonding” hypothesis. Nishida (Nishida et al. 1992; Nishida and Hosaka 1996) provided data to support the idea that males trade meat with other males in order to develop and maintain the alliances that are thought to play an important role in male-male competition for status. Mitani and Watts (2001) showed that, at least for the Ngogo chimpanzees, while the presence of a female with a sexual swelling was a significant predictor of the decision to hunt, this was an artifact of the relationship between the presence of such females and the number of adult males and that it was the number of adult males alone that predicted hunting. They also showed that males shared reciprocally, at least when considering all pairs of males simultaneously, and that there was a positive association between sharing of carcasses and support in agonistic coalitions (Mitani and Watts 2001; Watts and Mitani 2002).

By contrast, this hypothesis did not account for patterns of sharing between male chimpanzees at Gombe (Gilby et al. 2006). Hunting was more likely in parties with more males, but increasing male party size did not increase the likelihood that an individual focal male would hunt. Furthermore, these males did not share preferentially with those with whom they groomed or associated frequently (Gilby 2006). Similarly, an analysis of hunting among chimpanzees of the Kanwayara community found no support for this hypothesis, again using grooming and association as proxies for alliance partnerships (Gilby et al. 2008).

Hunting to Assess Reliability

Male chimpanzees vary in their hunting ability, as demonstrated by the proportion of hunts that they join, the number of kills that they make, and their success at hunting alone (Stanford et al. 1994; Stanford 1998; Boesch and Boesch-Achermann 2000; Watts and Mitani 2002). Among the Ngogo chimpanzees, and potentially elsewhere, good hunters are also more frequent members of the territorial patrols that monitor and probe boundaries with neighboring communities. Furthermore, males that hunt together patrol together, and the frequency of joint patrolling is correlated with the frequency with which males form coalitions and the amount of grooming between them (Watts and Mitani 2001, 2002). This leads to the hypothesis that hunting itself may have a function that is independent from acquiring meat: it demonstrates risk-taking and allows males to assess the reliability of others when faced with danger (Watts and Mitani 2001). This is essentially a refinement of Kortlandt's (1972) "hunting-to-display-social-prowess" hypothesis.

Given the risks associated with patrolling and intercommunity encounters (Goodall et al. 1979; Boesch and Boesch-Achermann 2000; Muller 2002), these kinds of mutual assessments may be important for male chimpanzees. The "hunting-as-risk-assessment" hypothesis might apply to the monkey-hunting specialists of the Taï Forest, as it appears to apply to the Ngogo chimpanzees, although it will be necessary to disentangle "hunting to assess reliability" from "male social bonding" (meat for allies) in testing the relative importance of these two ideas at both sites. This hypothesis may be interesting to consider in relation to the "show-off" hypothesis proposed to explain hunting behavior in human males (Hawkes 1991; Hawkes and Bird 2002).

So Why Do Chimpanzees Hunt?

The possibility that chimpanzees achieve nutritional benefits directly from hunting cannot be easily dismissed. The necessary nutritional studies quantifying chimpanzee diet have not been conducted, and for either of the trade-goods hypotheses to operate, there must be a nutritional gain to the individuals who receive and consume parts of the carcass. If there were not, the carcass would hold no value and could not be traded.

While it appears that chimpanzees hunt to gain meat, this is not to compensate for nutritional shortfalls. There is also essentially no support for the meat-for-sex trading hypothesis, and this can be largely discounted. That said, Gomes and Boesch (2009) found some evidence for this over a longer term (i.e., not in the immediate sharing context) among the Taï chimpanzees, which remains intriguing. The one context where females refrain from their promiscuous mating strategy is the consortship mating context (Tutin 1979). Does previous meat sharing by males increase the likelihood that females will comply with male efforts to initiate or maintain consortships? This remains to be determined.

While it seems that nutritional (i.e., calorific) gain appears to be sufficient to explain hunting in West African chimpanzees (at least at Taï: Stanford 1998) given the pattern of sharing in relation to participation, evidence that 47 % of individuals sharing a carcass appear to cheat the system (Boesch and Boesch-Achermann 2000), as well as the possibility that other factors influence hunting, needs investigation before any firm conclusions can be drawn. For the Ngogo chimpanzees, there is evidence for both the male social bonding and assessing reliability hypotheses. For the Gombe chimpanzees on the other hand, sharing appears to come down to successful harassment of those individuals possessing meat (begging), and there is no support for the male social bonding hypothesis.

The adaptive value – the function – of hunting thus remains unclear. Future work will need to consider variation in both predator and prey demography and perhaps determine more precisely the nutritional gains and energetic costs of hunting. It may also be worth testing hypotheses that address the behavior directly, rather than looking for a function in terms of relationships. It is becoming clear that chimpanzees hunt monkeys more frequently in locations where hunting costs are lower or at least where the prey should find it harder to escape; that hunting typically occurs when other food is abundant, such that hunters can absorb the calorific costs of failure; and that hunters who secure meat can gain substantial quantities in any particular bout. The question that needs to be addressed is whether the additional nutrition gained from meat translates into fitness: is there a direct fitness benefit to hunting?

Marginal Gains

McGrew (1992) showed that female chimpanzees who were more successful at gaining meat had greater numbers of surviving offspring, but it remains unclear whether males who gain more meat also derive fitness benefits. While it seems unlikely in calorific terms (there is no support for the energy shortfall hypothesis), there may be particular nutrients that are valuable, as suggested by the "meat-scrap" hypothesis. That hypothesis, however, focuses specifically on micronutrients, considering macronutrients such as protein and fat merely as helping to reduce dietary bulk (Tennie et al. 2009), and, with its focus on the minimum threshold, encounters problems explaining the variation in hunting between communities: if obtaining these micronutrients is critical, why are chimpanzees from communities where meat eating is rare able to maintain health and fertility? If the threshold is so low that these chimpanzees can reach it, why do then chimpanzees hunt substantially more frequently elsewhere?

The route out of this conundrum is to recognize that fitness is relative and that for male chimpanzees their primary reproductive competitors are the other males of their community. Thus, any benefits of meat eating need to be evaluated against these rivals, rather than in absolute terms. Here, I propose a new hypothesis that broadens the "meat-scrap" hypothesis as well as recognizes this relative nature of fitness. This new "marginal gains" hypothesis assumes (1) that meat is valuable specifically for *both* macro- *and* micronutrients, rather than its calorific value, and (2) that individuals benefit through marginal gains over their competitors.

For instance, small amounts of high-quality protein may provide an edge in sustaining muscle mass and thereby improving success in competing for high social rank. This "marginal gains" hypothesis predicts that individuals should value even the smallest scraps, as there is no threshold, and should attempt to gain more than rivals.

"Marginal gains" is therefore consistent with patterns of begging and food sharing seen in East African chimpanzees: individuals without meat are strongly motivated to acquire whatever they can, yet males gain over their rivals by not sharing and so need to suffer harassment costs before sharing. In communities where males willingly share with alliance partners, the need for allies may also outweigh any marginal gains from consumption: it may be no accident that the strongest evidence for sharing with allies comes from the community (Ngogo) with the largest number of adult males. If marginal gains show diminishing returns, this would account for individuals relinquishing possession of kills after feeding and diminishing motivation to acquire and consume meat with the quantity ingested.

Parenting Effort

As a final note, even if there are no nutritional benefits to be gained by males, simply by virtue of hunting they create a resource supply (converting live prey into food) for females that would be otherwise unavailable. If, on average, the most successful hunters are also, for whatever reason, the most successful at fathering offspring, then hunting will function as a form of parenting effort (as has been suggested for male chimpanzee territoriality: Watts and Mitani 2001) without any need for active sharing or provisioning by males. The natural variation in hunting and meat eating within and across chimpanzee communities should provide the opportunity to test such ideas, and more detailed, cross-site studies are needed.

Conclusions

Chimpanzees are not the only primates that hunt vertebrate prey. Baboons (*Papio* spp.) also hunt opportunistically, targeting small ungulates (Morris and Goodall 1977; Strum 1987), while red-tailed monkeys (*Cercopithecus ascanius*) stalk green pigeons (*Treron calva*) (Furuichi 2006). Among New World primates, capuchin monkeys (*Cebus* spp.) prey upon a variety of species with *Cebus capucinus*, perhaps best studied, showing a focus on squirrels, infant coatis, and birds (Rose 1997; Rose et al. 2003), while some squirrel monkeys (*Saimiri* sp.) hunt bats (Boinski and Timm 1985; Souza et al. 1997).

Among the great apes, vertebrate predation appears to be rare or absent in both gorillas and orangutans, although bonobos (*Pan paniscus*), the phylogenetic sister species to chimpanzees, do hunt vertebrates. Recorded prey species include black and white colobus (*Colobus angolensis*), red-tailed monkeys (*Cercopithecus ascanius*) (Sabater Pi et al. 1993), bushbabies (*Galago demidovii*) (Hohmann and Fruth 2008), flying squirrels (Kano and Mulavwa 1984), and forest duiker (*Cephalophus* spp.) (Hohmann and Fruth 1993; Fruth and Hohmann 2002).

Hunting by bonobos typically occurs at a lower rate than in chimpanzees: Fruth and Hohmann (2002) report only nine kills in 46 months of observation, seven of which were duiker, although data from the Lui Kotale site shows higher rates of predation: 18 kills in 60 months of observation (Hohmann and Fruth 2008).

While hunting is thus not unique to chimpanzees among the primates, it does appear to be a ubiquitous aspect of their behavior, occurring in all populations studied thus far. The picture that has emerged from these studies is one of diversity but with some common themes. Across populations, hunting is a predominately male activity. Chimpanzees hunt a variety of vertebrate prey, but there is a common focus on medium-sized mammals, particularly primates, and especially colobus monkeys. Red colobus appear to be the preferred prey, although the species (and body size) of red colobus varies across Africa. Chimpanzees appear to impose significant predation pressure on their main prey species, but the intensity and frequency of hunting vary between populations and from month to month within single communities. Hunting is typically opportunistic on encountering potential prey, although there is some evidence of searching. Hunts can be solo or group efforts, and the degree to which individual chimpanzees hunt together varies between East and West African populations. This appears to be related to the way the kill is divided following the hunt. In West Africa, the kill tends to be shared according to participation in the hunt and individual hunters collaborate, taking different roles, whereas in East Africa, the kill is often consumed selfishly or shared under pressure and may be shared with other males in the hope of future coalitional support; group hunts are more akin to multiple, simultaneous individual efforts to secure prey. In both East and West African populations, the presence of particularly skilled or motivated "impact" hunters increases hunting frequency and success.

It is important to recognize that this picture comes largely from detailed systematic studies of only a handful of communities (Gombe, Mahale, Taï, Ngogo, Kanyawara). Comparable systematic studies of hunting by chimpanzees in other populations are lacking, although some data are available from almost every population studied. In addition, much of the research effort has focused on chimpanzees and red colobus monkeys. Far less is known about chimpanzee hunting of other species and the nature and importance of hunting in populations that are not sympatric with red colobus. Certainly, chimpanzees without red colobus to hunt appear to hunt less frequently (Basabose and Yamagiwa 1997; Newton-Fisher et al. 2002), and it is unclear what impact low levels of hunting, providing fewer carcasses to share and consume, have on patterns of chimpanzee behavior.

Addressing these shortcomings is essential if we are to use an understanding of chimpanzee hunting behavior to shed light on the behavioral ecology of the hominins. The ubiquitous nature of chimpanzee hunting, the common occurrence of food sharing, and the diversity in the patterns of these behaviors, together with the close phylogenetic relationship between chimpanzees and humans, ensure that consideration of chimpanzee hunting is essential in any discussion of the role played by meat eating and food sharing in the behavioral ecology of early hominin species. The radiation of early hominins encompassed a number of species with different morphologies, and it seems likely that these hominins showed both within and between species variation in habitat and behavioral ecology (Foley 1997). The chimpanzee-red colobus system may be a useful model for some of that variation, but it remains necessary to understand the role of hunting and meat eating across chimpanzee populations, including those with an impoverished resource base. Already it is clear that different populations target different arrays of species, specialize or generalize their choice of prey, and hunt and use meat in different ways. Future studies of new populations are likely to increase this picture of diversity, and systematic tests of the hypotheses for hunting and meat sharing will clarify both why chimpanzees hunt and the importance of this behavior for the study of human evolution.

Cross-References

- ▶ Dental Adaptations of African Apes
- ▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
- ▶ Great Ape Social Systems
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ Modeling the Past: The Primatological Approach
- ▶ The Species and Diversity of Australopiths

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Cooperation, Coalition, Alliances

Charlotte K. Hemelrijk, Ivan Puga-Gonzalez, and Jutta Steinhauser

Contents

Abstract

In primates, cooperative acts have been observed such as communal rearing of offspring, cooperative mobbing of predators, supporting others in fights, and grooming others. Grooming builds up a social bond between the partners, helps in repairing relationships, and produces all kinds of benefits for the groomee, such as the reduction of parasites and of tension. Although the costs for the groomer are low, it has been regarded as an altruistic act and therefore is expected to be preferably directed toward kin or to be repaid by being reciprocated or exchanged for another service (e.g., support in fights, help in rearing offspring in the case of communal breeding systems, or access to some object, such as food, or some individual such as a female, an infant, or members of another group).

C.K. Hemelrijk (✉) • I. Puga-Gonzalez • J. Steinhauser
Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies,
University of Groningen, Groningen, CC, The Netherlands
e-mail: c.k.hemelrijk@rug.nl; i.puga-gonzalez@rug.nl; j.steinhauser@rug.nl;

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The formation of coalitions may result in the maintenance or in the increase of the dominance of an individual, in the expulsion of certain individuals from a group, in taking over a group, in the defense of the home range against other groups, in getting access to estrous females, and in the protection of an infant or adult female. The degree of cognition involved in coalitions is unclear.

Which members of a group cooperate differs from species to species; it may be influenced by genetic and social relationships, by the size and the composition of the group (the sex ratio), by the degree of competition, and by the distribution of food.

Introduction

Cooperation in primates varies greatly among members of a group. For instance, individuals groom the fur of others, help others in fights, collect food together (for communal hunting in chimpanzees, see chapter "▶ The Hunting Behavior and Carnivory of Wild Chimpanzees," Vol. 2), share food, and may help in raising the offspring of others. Furthermore, group members cooperate against danger from the outside. They mob predators together and form coalitions to defend their home range against other groups.

For a long time, behavioral acts such as coalition formation, grooming, and food sharing have been regarded as "altruistic" (costing the actor more than it receives), and therefore, the main explanations have been the theories of kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971). However, it has become increasingly clear that these supposedly altruistic acts are beneficial for both cooperation partners. For instance, grooming not only reduces tension in the receiver but also in the performer (Shutt et al. 2007), and grooming a high-ranking individual serves as a protection against aggression for the subordinate. Coalition partners may increase their access to fertile females or help maintain their status quo within the dominance hierarchy. Furthermore, whereas coalitions were originally supposed to require high cognitive abilities, it is increasingly acknowledged that these patterns may arise from simple behavioral rules (as for cognitive mechanisms, see also chapters "▶ Evolution of the Primate Brain," Vol. 2, "▶ Great Ape Social Systems," Vol. 2, and "▶ Primate Intelligence," Vol. 2). Besides, cooperation depends on the social system and the kind of primate involved (such as Old World monkeys vs. New World monkeys). We will treat these aspects below.

Social System

Cooperation among individuals of a group depends on the species and its social system. There are many species of primates, and they live in many different kinds of social systems, as solitary individuals, monogamous pairs, single-male groups, multimale groups, or fission-fusion systems (see chapter "▶ Great Ape Social Systems," Vol. 2). In group-living species with many females, the males usually migrate and the females remain in their natal group for life (female-philopatry), e.g., baboons, macaques, and vervets. Wrangham (1980) refers to these species as “female-bonded,” because the females are more kin related than the males. In such groups, female social relationships and cooperation are developed much further than among the males of the group and also further than among females of species that are not female-bonded, the so-called female-transfer species. In line with this, grooming reciprocation among individuals of the resident sex is higher than among those of the sex that transfer (Hemelrijk and Luteijn 1998). In chimpanzees, for instance, males stay together and females migrate. Here, relationships among males are more cooperative than among females (male bonded). Greater cooperation among the resident than the migrating sex has been attributed to the closer relatedness of the resident sex. Evidence for closer relatedness in the resident sex is found among macaques (Ruiter 1998) and chimpanzees (Goldberg and Wrangham 1997). Although it has also been argued that male chimpanzees that cooperate are more often more closely related than those that do not, this is not supported by evidence from DNA-typing methods (Goldberg and Wrangham 1997; Langergraber et al. 2007). Furthermore, social relationships differ between Old World monkeys and New World monkeys: among Old World monkeys, they are more developed (Dunbar 1993). The causes of these differences are unknown.

Grooming

Grooming occurs in all primate species (Goosen 1987), and of all affiliative social acts, it is the one that is displayed most frequently. It consists in picking through the fur to remove parasites and to clean small injuries. An individual may clean its own fur (autogrooming) or that of another (allogrooming). Because allogrooming is a social act, it has sometimes been questioned whether it has any cleaning function at all. That allogrooming actually aims at cleaning is shown by Zamma (2002): Japanese macaques groom more often those spots of others and of themselves that tend to house more lice and eggs. Furthermore, in his study of 17 spots on the bodies of 19 species of primates, Barton (1985) has shown that individuals groom others particularly at spots that they themselves cannot easily reach. Therefore, spots on the skin that are groomed more often by others are groomed less often by the individual itself and vice versa.

Since in species that live in larger groups, individuals spend more time grooming, grooming clearly also has a social function (Dunbar 1991, 2003). Note that this correlation with group size appears more clearly among Old World monkeys than among New World monkeys. This may arise because coalition formation is more important in Old World monkeys and grooming may be helpful in building up alliances. In line with this, it has been found that individuals groom more often those partners they also support more frequently. This has been observed in several species such as female chimpanzees (Hemelrijk and Ek 1991), male chimpanzees (Watts 2002), gorillas (Watts 1997), baboons (Seyfarth 1976; Smuts 1985b), female vervet monkeys (Seyfarth 1980), and several species of macaques (Hemelrijk 1994; Kapsalis and Berman 1996; Schino et al. 2007; Silk 1992b; Ventura et al. 2006).

Grooming relationships among males of the genus *Macaca* (Hill 1994) and among females of a number of female-bonded species (Hemelrijk and Luteijn 1998) are influenced by the identity of the migrating sex and by the composition of the group, namely, the sex ratio. As to the sex ratio, it has been shown that food provisioning led to a female-biased sex ratio in a number of groups of species of the genus *Macaca* (Hill 1994, 1999). This arose because provisioned food was offered in clumps and thus led to stronger competition, and this drove several males away. Groups that were not provisioned had a more equal sex ratio, because in these groups, competition for concentrated food sources was less. This may have allowed males to be friendlier among themselves and groom each other more often. Further, in the case of an even sex ratio, more grooming among males may arise because the number of males to be groomed is greater and the number of females to groom with is smaller than in groups with a female-biased sex ratio. This results in a higher number of potential male partners to affiliate with and therefore more affiliation among males. Among females, grooming relationships seem to be influenced by competition for access to males. In a large comparative study of female-bonded species of primates, Hemelrijk and Luteijn (1998) discovered that the degree of reciprocation of grooming among females increased with the increase in the relative number of adult males in the group. This was attributed to female competition for access to males; the lower the number of males present, the stronger the competition among females to affiliate with males. This competition hindered females from building up good relationships among themselves. This argument is supported by the fact that grooming reciprocation increases more strongly with sex ratio among females in a single-male group (where sex ratio depends on group size) than in a multimale group. Even if the number of males increases in multimale groups, this increase is not entirely to the profit of the time the males have available for females. There are two reasons for this: first, because males will intervene in interactions of other males with females and second, because males will interact among themselves, which reduces the time available for positive social interaction with females. In single-male groups, however, interactions and interventions among males are lacking.

The positive effect of grooming on relationships is supposed to be a reduction of tension, increase of trust, and restoration of the relationship after a fight. As regards tension, grooming calms and relaxes the groomee and the groomer (Terry 1970; Goosen 1975; Shutt et al. 2007). In the groomee, the heartbeat slows down (Boccia et al. 1989) and the rate at which it shows a displacement behavior, such as scratching, decreases (Schino et al. 1988). Keverne and coauthors (1989) have shown that being groomed is pleasurable because it increases the concentration of endorphins in the brain. Grooming is supposed to maintain relationships in the light of competition, because hamadryas females with an established relationship are observed to groom each other more often if a dyad is accompanied by others than if the dyad is temporarily separated in cages (Stammbach and Kummer 1982). Furthermore, grooming is also supposed to restore a relationship: often after fights, the frequency of grooming and other affiliative behavioral acts between former opponents is higher than when no fights take place. This is known as "reconciliation" and has been shown to occur in species of all major radiations of primates (Aureli et al. 2002; Silk 2002). Being attacked implies that there is a high chance that more aggression will follow. Friendly postconflict reunions reduce this aggression and restore the relationship. This function appears from the elegant experiments by Cords (1992). She determined at what distance pairs of long-tailed macaques could drink next to each other without trouble. Then she showed that after aggression among the members of a pair, its ability to jointly exploit the resource was seriously reduced. If, however, after such a conflict, a friendly reunion took place, the use of the resource was completely restored to normal. Relationships are, however, not always damaged by aggression; the damage depends on the context in which the aggression takes place. In the case of competition over food, the relationship keeps its status quo even without reconciliation. Furthermore, the occurrence of reconciliation depends on the value of the relationship. According to the "valuable relationship hypothesis," reconciliation particularly occurs in relationships of great value (Aureli et al. 2002; Silk 2002). This theory is supported by the following experiment by Cords and Thurnheer (1993): when macaque partners are obliged to cooperate with each other to obtain food, they reconcile three times more often than when cooperation is not necessary. In line with this, reconciliation has been shown to occur more often in those relationships that are characterized by a high frequency of support (such as in macaques among members of a matriline; and in gorillas reconciliation occurs in the cooperative relationship between the sexes rather than among females (Watts 1995a, b)). Further, in general, more friendly postconflict reunion occurs among those individuals that exchange high levels of friendly behavior.

As to the cognition used in displaying reconciliation, there is debate. According to de Waal and Yoshihara (1983), the cognitive capacities needed are memory of the former opponent and conciliatory predisposition. On the other hand, the cognitive requirements must be slight because juveniles already reconcile in the same way as adults do (Aureli et al. 2002). No cognition specific for reconciliation is required however according to an individual-based model concerned with individuals that group, groom, and fight (GrooFiWorld, see Puga-Gonzalez et al. 2009). According to this spatially explicit model, statistically "reconciliation" is observed, because former opponents are closer after a fight than they are on average otherwise. Consequently, former opponents have more opportunities to groom each other after a fight than otherwise. Since individuals are more likely to groom partners that are close by and to groom others when they themselves feel stressed (which individuals do after a fight), this results in behavior which primatologists have labeled reconciliation. Thus, empirical studies should control for effects of proximity. Indeed in the few empirical studies that controlled to some degree for proximity, the rate of reconciliation was significantly reduced (Call 1999; Call et al. 1999; Majolo et al. 2009; Matsumura 1996). Another reason to take the need for further control of proximity seriously is that the model GrooFiWorld also shows that the reconciliation-like behavior happens, like in empirical data, more often among "valuable relationships." Yet, individuals in the model are not aware of who their friends are. Further, like in empirical data, reconciliation-like behavior in the model is more frequent in egalitarian than in despotic societies. In the model, this is a side effect of the relative rate of grooming versus fighting which is higher in egalitarian than in despotic societies; in empirical data, it was supposed to be caused by a greater uncertainty about dominance relationships in egalitarian societies.

Further, it has been shown that the frequency and stability of grooming relationships over time have a positive impact on the fitness of the individual. For instance, in a population of wild baboons studied over 15 years, Silk and coauthors (Silk et al. 2010, 2003, 2009) show that strong social bonds among females increase their life span and that of their offspring. This effect was independent of dominance rank and environmental conditions. Similarly, in a study of wild Assamese macaques, the strength of the social bonds among males appeared to be directly and positively related to the number of offspring they sired (Schuelke et al. 2010).

Grooming: Kin Selection, Reciprocation, and Exchange

Grooming does not only lead to social bonding but may also be considered an altruistic trait because of the costs to the actor and the advantage for the receiver. Although its cost (expenditure of energy) is low (Wilkinson 1988), grooming may cost time that might be used for (a) vigilance and (b) foraging. Two studies report a decrease in vigilance, one among captive rhesus monkeys and the other among wild blue monkeys. In rhesus macaques, mothers become less vigilant during grooming, and consequently their infants were more often harassed by group members (Maestripieri 1993). Blue monkeys became significantly less watchful of predators when grooming than when foraging or resting (Cords 1995). Grooming does not diminish time for foraging (Dunbar and Sharman 1984): in two species of baboons (olive baboons and gelada baboons), increased foraging time was associated with a decrease in the length of time spent resting, but time spent grooming remained the same. This may be an indication of the importance of grooming. Indeed, baboons and macaques devote up to 20 % of their time to grooming others (Dunbar 1988).

Within the framework of grooming as an altruistic act, the distribution of grooming partners can be explained either by the theory of kin preference (Hamilton 1964) or by reciprocal altruism (Trivers 1971). In support of kin selection, the most intense grooming bonds are found between mother and offspring, and in general in most primates, individuals aim their grooming primarily at their kin (Gouzoules and Gouzoules 1987; Schino 2001).

When altruistic acts are directed toward unrelated individuals, the expectation is that something should be received in return (Trivers 1971). Recent models suggest that parceling of grooming bouts in small periods, in which the role of actor and receiver alternates, is a method of achieving reciprocation (Connor 1995). During a certain part of their grooming bouts – ranging from 5–7 % for *M. radiata* (Manson et al. 2004) to 74 % in *Callithrix jacchus* (Lazaro-Perea et al. 2004) – partners groom each other alternately. In grooming bouts of female chacma baboons, where both partners groom each other in turn, the total grooming duration by both partners is indeed significantly correlated between bouts (Barrett et al. 1999, 2000). Similar findings were made in white-faced capuchin monkeys and bonnet macaques (Manson et al. 2004) but not in Japanese macaques (Schino et al. 2003).

Furthermore, it was argued that the time during which an individual grooms another should increase as a sign of the increasing trust among partners (model of "raise the stakes," Roberts and Sherratt 1998). Increasing bout lengths have not, however, been confirmed in empirical studies of either capuchin monkeys or baboons (white-faced capuchins, Manson et al. 2004; chacma baboons, Barrett et al. 2000). Instead in chacma baboons, bout length even decreased over time.

Grooming may either be reciprocated for its own sake or interchanged for another service, e.g., support, reduction of aggression, or access to something or someone (such as food, a female, an infant, or another group) or support in rearing offspring (in communal breeding systems). Here, a major problem is how to define reciprocation operationally. Reciprocation and interchange may be considered as a correlation between the number of times each individual gives something to a partner and how often it receives this service from him/her in return. This summed value over a period of time may be studied at the group level, the so-called actor-receiver model (Hemelrijk 1990a, b). Reciprocation in grooming occurs in many species, for instance, among both males and females in chimpanzees in captivity (Hemelrijk and Ek 1991) and among male chimpanzees under natural conditions (Watts 2000a), among female Samango monkeys (Payne et al. 2003), blue monkeys (Rowell et al. 1991), baboons (Seyfarth 1976), marmosets (Lazaro-Perea et al. 2004), female Japanese macaques (Schino et al. 2003), and gorillas (Watts 1994). Such a correlation of reciprocation may, of course, occur as a side effect of other correlations. For instance, when higher-ranking individuals groom others more often and when everyone grooms others more often according to the rank of the partner, grooming reciprocation follows automatically (Hemelrijk 1990b). To exclude such alternative explanations, partial matrix correlations are useful (Hemelrijk 1990a). Both in chimpanzee males and females (Hemelrijk and Ek 1991; Watts 2002) and in savanna baboons (Seyfarth 1976; Hemelrijk 1991), grooming reciprocation remained significant even after partialling out the effect of other variables such as dominance and support. In other studies, grooming reciprocation was present while controlling for kinship (hamadryas baboons, Stammbach 1978; vervet monkeys, Fairbanks 1980; Japanese macaques, Muroyama 1991). Only in a few studies no reciprocation of grooming was observed (bonobos, Franz 1999). Recently, reciprocation of grooming among female primates was confirmed in a meta-analysis of 48 groups of 22 species. Results remained significant even after controlling for kinship (Schino and Aureli 2008a).

Apart from being reciprocated, grooming may also be exchanged for other services. For instance, Seyfarth (1977) argues that higher-ranking females are more attractive to groom because from them more effective support in fights can be expected in return. Since females will compete to groom the highest-ranking partners, and since higher-ranking females will win this competition, each female will in the end groom most frequently with those partners adjacent in rank and be groomed most often by those ranking just below her. Seyfarth used this model to explain the observation that in several female-bonded primate species, such as baboons (Seyfarth 1976), vervets (Fairbanks 1980), and stump-tailed macaques (Estrada et al. 1977), females aimed at grooming up the hierarchy and mainly at those that were next in hierarchy (Seyfarth 1980). Since then, these patterns have statistically been studied in many species. In a number of them, particularly Old World monkeys (such as certain species of macaques, e.g., rhesus monkeys (Kapsalis and Berman 1996), chimpanzees (Hemelrijk and Ek 1991; Watts 2000b), and bonobos (Franz 1999; Vervaecke et al. 2000)), these patterns were, at least partly, confirmed, but in others evidence is lacking, for instance, in female langurs (Borries et al. 1994), in blue monkeys (Cords 2000, 2002), and in New World monkeys, such as wedge-capped capuchins, *Cebus olivaceus* (O'Brien 1993), and tufted capuchins, *Cebus apella*, in both wild (Di Bitetti 1997) and captive colonies (Parr et al. 1997; Schino et al. 2009), but not always (see Tiddi et al. 2012). There was even a trend against grooming higher-ranking animals because individuals groomed down the hierarchy among capuchins and in callitrichids (Lazaro-Perea et al. 2004). In callitrichids, this is suggested to have a function in the communal breeding system: the breeding female (i.e., the alpha-female) uses grooming to make lower-ranking individuals stay in her group in order to help her bring up her young.

Furthermore, the relation between grooming and the receipt of support is doubted. Although correlations were found in studies of several species, such as vervets (Seyfarth 1980), baboons (Seyfarth 1976; Hemelrijk 1990a), female chimpanzees (Hemelrijk and Ek 1991), male chimpanzees (Watts 2002), bonobos (Vervaecke et al. 2000), capuchins (O'Brien 1993), and one group of bonnet macaques (Silk 1992a), they were lacking in an earlier study of the same group of bonnet macaques (Silk 1982), in rhesus macaques (de Waal and Luttrell 1986), and female baboons (Silk et al. 2004). The relation is supported by two experimental studies dealing with vervets and long-tailed macaques. Seyfarth and Cheney (1984) recorded a call of vervets that seems to solicit support from others. They played it back to individuals of a natural colony of vervets that had recently been groomed by the caller and to others that had not. The length of time individuals looked up at the speaker was considered to be an indication of the tendency to support the caller. Among nonrelatives, individuals looked at the speaker longer when the caller had recently groomed them. In this experiment, it remains uncertain, however, whether looking up at the speaker actually indicates a readiness to support him or her. Therefore, in an experiment with long-tailed macaques (Hemelrijk 1994), actual support was measured directly. Trios of females were separated from the group. After two high-ranking individuals had been given the opportunity to groom, a fight was provoked between one of them and a low-ranking female. The frequency with which the third high-ranking female intervened in the fight was counted. The third female appeared to support only the other high-ranking female, and she did so more often after she had been groomed by her than if not. This supports the notion of a relationship between being groomed and supporting. It is not definitive evidence for an exchange, however, because being groomed may increase the tendency to support in general, even on behalf of those by whom the supporter was not groomed at all. Furthermore, individuals appear to support the aggressor but not the victim; therefore, it is as yet unknown whether a similar association with grooming holds also for victim support (which is more risky). Besides, these experiments do not show whether varying amounts of grooming lead to varying amounts of support. A recent meta-analysis of grooming and support based on 36 studies from 14 species of primates, Schino (2007) states that pairs of females that groomed each other preferentially also supported each other more. However, in this study, it was not specified whether grooming was given or received, and thus it is not clear whether an actual positive correlation for the exchange between grooming and support exists at all in their data.

Henzi and Barrett (1999) suggest that the receipt of support is not the major benefit of grooming because grooming occurs also among females that do not support at all, for instance, in certain groups of chacma baboons (in the Drakensberg). Instead, they argue that the short-term benefit of grooming is the decrease risk of aggression and harassment from others during the grooming bout itself (as suggested for bonnet macaques (Silk 1982) and capuchin monkeys (O'Brien 1993)), because support is rare in female-bonded species, although those females groom each other. Further, Henzi and Barrett (1999) argue that the degree to which grooming should be reciprocated or exchanged for something else depends on the competitive regime; when resources are widely distributed and cannot be monopolized, competition is weak, individuals equal each other in power, and grooming should be reciprocated. If resources can be monopolized, however, competition is intense, power differences are great, and grooming should be exchanged for increased access to resources. In line with this, in a comparison between groups and in a study of the changes in the same group over time, grooming appears to be reciprocated if competition is weak rather than intense (Barrett et al. 1999, 2002). Similarly, in a meta-analysis (Schino and Aureli 2008b) and in an individual-based model (Puga-Gonzalez et al. 2009), grooming reciprocation becomes weaker when the dominance hierarchy is steeper (thus competition is stronger). For this, different cognitive explanations are given. Schino and Aureli (2008b) argue that individual primates adjust their distribution of grooming depending on their competitive regime. According to the computational model, GrooFiWorld model (Puga-Gonzalez et al. 2009), reciprocation of grooming is directly influenced by the asymmetry of risks of losing a fight from an opponent. Here, reciprocation of grooming decreases if the hierarchy is steeper because high-ranking individuals experience less risk in attacking the lower-ranking ones, and therefore, they are more likely to attack them than to groom them, whereas for the lower-ranking ones, the opposite holds. Conversely, if the hierarchy is weaker, risk asymmetries are smaller and individuals are more similar in their tendency to attack and groom each other. A third explanation for the decrease of reciprocation of grooming when competition is more intense is found in the fact that intense competition is associated with a sex ratio that is more skewed toward adult females. Weaker grooming reciprocation in groups with more females has been discovered in several primate species by Hemelrijk and Luteijn (1998) and is attributed to stronger competition among females for access to males. Note that differences in degree of competition for access to males may also explain the pattern of grooming reciprocation in the baboons studied by Barrett and coworkers.

Grooming is also supposed to be exchanged for access to food. The best evidence for this comes from two experiments, one with long-tailed macaques by Stammbach (1988) and the other with vervet monkeys by Fruteau et al. (2009).

In both studies, authors trained individual members of a group to become experts in operating a food apparatus. During the period in which it was the expert, this individual appeared to be groomed significantly more often.

Note that “food sharing” in primates almost exclusively means passive tolerance toward others when others take away a bit of food and that active giving is extremely rare (McGrew 1992). In a food exchange experiment among captive chimpanzees, de Waal (1997) found some evidence that females allow others to take away food more easily if they have been groomed by them in the preceding 2 h than if not. Food sharing and its reciprocation seems, however, largely a matter of mutual tolerance rather than intentional reciprocation, as is shown in experiments with brown capuchin monkeys (Waal 2000).

If males groom females, this is further supposed to increase a male’s access to mating partners and thus reproductive success, for instance, in chimpanzees, baboons, and rhesus monkeys. In chimpanzees, this has been regarded as a kind of “bargaining for sex” (Goodall 1986). For instance, Gumert (2007) shows that male long-tailed macaques groomed preferentially those females with whom they mated more. Similarly, chimpanzee males groomed more often those females with whom they mated more frequently mainly during the period of female tumescence; this relation, however, resulted neither in a long-term bond (Hemelrijk et al. 1992) nor led to more offspring from the females that were groomed more often by the male (Hemelrijk et al. 1999; Meier et al. 2000). Hence, male grooming of females may simply function to calm down the male’s aggressive tendency or the tendency of the female partner to flee, and therefore, it need not be considered as a kind of exchange or currency. Furthermore, male rhesus monkeys mainly groom females during the mating season, and captive females prefer males who groom them most (Michael et al. 1978); yet, there are no long-term reciprocal bonds between the sexes (Maestripieri 2000). Long-term sociopositive relationships between males and females have been described, however, for savanna baboons (Seyfarth 1978a, b; Smuts 1985b; Palombit et al. 2000).

In several species, grooming and embraces are used to get access to newborn infants, e.g., in baboons (Rowell 1968; Frank and Silk 2009), patas monkeys (Muroyama 1994), moor macaques (Matsumura 1997), sooty mangabeys and vervet monkeys (Fruteau et al. 2011), and spider monkeys (Slater et al. 2007). Furthermore, if low-ranking female chacma baboons want access to a newborn from a higher-ranking mother, they need to groom the mother longer in proportion to the size of the difference in rank (Henzi and Barrett 2002).

Coalition Formation

Here we deal only with those coalitions that are targeted at other group members and not at other groups (for coalitions against other groups, see section “Collective Defense of Home Ranges”). A coalition (or alliance) is a coordinated attack by two or more individuals (the coalition partners or allies) on one or more opponents, the so-called targets (Chapais 1995). Coalitions may start in several ways: two individuals may attack a common victim, a coalition partner may spontaneously participate in an ongoing fight, or it may join after being enlisted by one of the combatants. Several types of coalitions are distinguished on the basis of their form and their effect (Chapais 1995; van Schaik et al. 2004). As regards form, the distinction is between coalitions of members (a) that rank above the target (called "all-down"), (b) that rank below the target (called "all-up"), or (c) of which one ranks above the target and another below it (called "bridging" coalitions or alliances). As regards effects, a distinction is made between (a) alliances that reinforce the existing rank order and therefore are "conservative"; (b) coalitions that cause one individual to change rank and thus are "rank changing"; or (c) coalitions that cause more individuals to change rank, e.g., when two lower-ranking individuals defeat a top male, and thus are "revolutionary." Coalitions usually involve three individuals (a triad), but more individuals may participate (a polyad).

As regards the cognition involved in the formation of coalitions, opinions differ. Harcourt (1988) suggests that primates form coalitions for strategic reasons and that they must take into account a complex set of information about their own power and that of their allies in comparison to that of their opponent and allies. For instance, when recruiting support, an individual should not only be aware of the social relationships between itself and other individuals but also of the relationships among the other individuals, so-called triadic awareness (Harcourt and de Waal 1992; Paxton et al. 2010; Schino et al. 2006; Silk 1999). Along these lines, in a comparative study between a captive group of long-tailed macaques and one of chimpanzees, coalitions of chimpanzees appeared to be more frequent and larger than those of macaques, and this was considered as an indication of their greater cognition (de Waal and Harcourt 1992). Others argue, however, that coalition behavior may develop with little planning and anticipation of the results because individuals may passively learn to recognize the advantage of joining forces (Chapais 1995). Along similar lines, the pattern of coalitions in sooty mangabeys and Barbary macaques may result from simple behavioral rules such as "support the higher-ranking individual in a conflict," "solicit support from potential allies that outrank yourself and the target," and "choose the strongest partner at hand" (Range and Noë 2005; Bissonnette et al. 2009). The simplest cognition involved in coalitions is given in a modeling study of individuals that group and attack each other diadically (Hemelrijk and Puga-Gonzalez 2012). Here incidental coalitions were observed following the empirical definition of coalitions, namely, that after a fight between two individuals, a third nearby individual attacked one of the former opponents. Remarkably, these incidental coalitions are of the three different types (i.e., conservative, bridging, and revolutionary) with a frequency of occurrence similar to that in empirical data.

During fights, individuals may display so-called enlisting behavior by which they seem to try to attract others into the fight. This may consist of a rapid movement of the head between the opponent and the individual from whom help is requested, called "headflagging" and "pointing" (de Waal et al. 1976; Noë 1992; Silk 1999). Male bonnet macaques recruit support via "headflagging" with a success rate of 24 % (Silk 1999). In chimpanzees, several behavioral actions are shown by fighting animals to a third individual that is not (yet) involved in the fight, and these are indicated as "side-directed behavior" (de Waal and van Hooff 1981). One action is the so-called "hold-out-hand" gesture in which an individual stretches out its hand toward a potential helper (de Waal and van Hooff 1981). The effectiveness of such solicitation behavior in chimpanzees is unclear. In contrast to the positive results by de Waal and van Hooff (1981), in another study of the same colony by Hemelrijk et al. (1991), most support was obtained without preceding side-directed behavior, and it was clear that side-directed behavior was not a precondition for acquiring help in fights. Besides, side-directed behavior was rarely followed by support, and there was no indication that it increased the chance of receiving help. Note that also if the analysis was confined to cases of hold-out-hand behavior, hold-out-hand appeared not to result in obtaining support. This is in line with the experimental observations of chimpanzees by Hare and coauthors (2004): they discovered that chimpanzees are unable to understand pointing toward an object (Tomasello et al. 1997) but that chimpanzees easily anticipate the stretching arms of those who want to take away something that is of interest to them. Thus, it appears that they are better equipped to compete than to cooperate. Side-directed behavior is mostly displayed by females when they are threatened and is significantly concentrated on higher-ranking individuals; thus, side-directed behavior may be beneficial to the soliciting individuals in the sense that it tends to bring them nearer to a high-ranking individual, which may have a protective effect as a threat to the original opponents (Hemelrijk et al. 1991).

In interventions in fights, it is usually the aggressor and the winner of the fight that is supported. This is less risky than supporting the victim. Notable exceptions are mothers supporting their offspring (see section "Youngsters") and the "control role" of the alpha-male. For instance, in a captive colony of Japanese macaques (Watanabe 1979), the alpha-male more often than other males supports aggressees, in particular babies and youngsters, against adults. This is called a "control role." A similar control role in the form of supporting losers is described for the alpha-male in gorilla groups by Watts (1997). Here, males intervene in fights among females. Because this may promote egalitarianism among females, the male may use it to keep females in his group. Male intervention hinders, however, the formation of alliances among females.

Functions of Coalition

As regards their function, Smuts (1987) distinguishes a number of main types of coalitions:

1. Coalitions to take over a single-male group: This has been reported for males of gray langurs (Hrdy 1977).
2. Coalitions among males to get access to an estrous female that is in consort with another male: These coalitions do not affect dominance relationship and are common in savanna baboons (Smuts 1985a). Coalition partners are typically of

middle rank (Noë and Sluijter 1995). Packer (1977) found that the male that enlisted help from another was the one to obtain the female, but in a later study, Bercovitch (1988) showed that males that were solicited were as likely to obtain the female as those that solicited, and Noë (1992) himself observed that both partners of a coalition may enlist each other's help simultaneously.

3. Coalitions to repel outside males: This has been reported among females as well as among males. Coalitions among males occur between groups of species living in single-male groups such as gorillas, hamadryas baboons, and gelada baboons. Coalitions among males of a single group have been described in multimale groups of chimpanzees, red colobus monkeys, spider monkeys, white-faced capuchin monkeys, and sometimes also among savanna baboons. In chimpanzees (Wrangham 1999; Wilson and Wrangham 2003) and white-faced capuchin monkeys (Gros-Louis et al. 2003), male coalitions may even result in killing an adult of another group.
4. Coalitions among females or between a male and a female to protect infants: Although the main protectors of youngsters are their mothers, in all species virtually all group members will defend an infant if it is in danger (for instance, against an attack by an adult male), and female baboons are even suggested to maintain close associations with particular males in order to be protected against aggression from males (Palombit et al. 2000, 1997).
5. Coalitions among females to protect an adult female against an attack by a male: Mobbing a male to protect a female may be useful for females (even unrelated ones) since it warns males that hostility to females is risky.
6. Coalitions to increase the dominance position of one or both member(s): Here, we will treat results for youngsters and for adults separately.

Adults

Coalitions to increase the dominance position among adults have been reported for Japanese macaques, rhesus, Barbary macaques, stump-tailed macaques, mantled howlers, red howlers, chimpanzees, and gray langurs.

When females are observed to attack males together, they are assumed to increase their dominance over males. This is mentioned for Japanese monkeys, rhesus monkeys, and bonobos (Chapais 1981; Thierry 1990; Parish 1994), and indeed in these species, certain females are dominant over certain males. Such coalitions may not be a precondition for female dominance, however, because a spatial model of individuals that group and compete (via dominance interactions) shows that female dominance can also arise only from competitive interactions in the absence of coalitions (Hemelrijk et al. 2003, 2008). According to this model, the stronger female dominance in bonobos compared to common chimpanzees may be due to their greater cohesion in grouping. Furthermore, stronger female dominance among rhesus macaques as compared to Celebes macaques (Thierry 1990) may arise from their higher intensity of aggression. Besides, also a higher percentage of males in the group increases intensity of aggression on average in the group and, herewith, female dominance relative to males. Both factors, cohesion and intensity of aggression, increase hierarchical differentiation; and this reduces the size of the initial difference in dominance between the sexes (Hemelrijk et al. 2003, 2008).

When males support females, males usually benefit in terms of dominance. For instance, in Japanese macaques, an alpha-male supported females of lower-ranking matrilines against the alpha-female with whom he had an unstable dominance relationship. Similarly, in rhesus monkeys and chimpanzees, females supported the alpha-male against other males, and in vervets support by females influenced dominance relations among males (Chapais 1995).

Among the three top-ranking males in chimpanzees, coalitions may induce changes of dominance in several ways. For instance, among wild chimpanzees, a top-ranking alpha-male (A) had an unstable relationship with the stronger beta (B). When the gamma-male (C) supported the alpha against the beta, (C) rose in rank above (B) (Nishida 1983). One-and-a-half years later, however, support by the now gamma-male to the alpha-male caused them (B and C) to reverse dominance again (Uehara et al. 1994). Thus, the gamma-male played out the alpha-male against the beta-male and this happened also in captivity (de Waal 1982).

In captivity, at other times, the beta-male and gamma-male were observed to join against the alpha-male (a revolutionary alliance). Thus, both rose in rank above the alpha-male (de Waal 1982). Such competition among males has sometimes fatal consequences (Watts 2004). Revolutionary alliances have further been described for male langurs, Barbary macaques, and rhesus macaques (Chapais 1995; Higham and Maestripieri 2010; Bissonnette et al. 2011). However, in none of these species did males form coalitions to obtain estrous females.

Youngsters

In a number of female-bonded species (Wrangham 1980), there is also a complex support system that provides young females with approximately the dominance rank of the mother. It has been called a “matrilineal dominance system” and a “nepotistic hierarchy,” because the support involves kin. The nepotistic hierarchy implies that all daughters rank immediately below their mother and that among sisters the youngest sister has the highest rank (so-called youngest ascendancy). This classical form of a nepotistic dominance hierarchy is found in rhesus macaques, Japanese macaques, and long-tailed macaques. The formation of hierarchies between matrilines has been investigated in a series of admirable experimental studies of Japanese and long-tailed macaques by Chapais and coworkers (Chapais 1995, 1996; Chapais et al. 2001; Chapais and Gauthier 2004). They created subgroups of three or six juvenile Japanese macaques (with one or two peers of the same matriline) and then added an adult. In this situation, a low-ranking juvenile female appeared to be able to outrank peers in the presence of closely related females but not in the presence of more distantly related kin, such as aunts, grandaunts, or cousins, due to lack of support from them. After female dominance over a lower-ranking matriline was “assigned,” it was maintained by mutual support among members of the same matriline against those of a lower matriline: from that time onward, the young females joined opportunistically in ongoing conflicts against lower-ranking females (called “the common targeting principle”).

Within matrilines, younger sisters become dominant over older ones, the so-called "youngest ascendancy" rule. This is caused by the mother's support of a younger daughter against her older ones. If the mother is absent, dominant unrelated individuals will also support younger sisters against older ones. Thus, the network of alliances of females extends beyond her kin.

However, in some groups, the matrilineal dominance system is incomplete (weakly nepotistic) (Chapais 2004). For instance, youngest ascendancy is lacking in some feral groups of Japanese macaques (Hill and Okayasu 1995), provisioned groups of Barbary macaques (Prud'homme and Chapais 1993), and one captive group of Tonkean macaques (Thierry 2000). Furthermore, in baboons, daughters may outrank their mother during adulthood (Combes and Altmann 2001). Chapais and Lecomte (1995) give three explanations of weak nepotism: demographic, (phylo)-genetic, and ecological.

The demographic explanation comes from a model by Datta and Beauchamp (1991), who simulated the effects of demography on female dominance relations by comparing two populations that differ in their growth rate. One population is growing fast (with 2.8 offspring per female) and the other is declining (with 0.6 offspring per female). Thus, in the declining population, matrilines are smaller, and potential allies are fewer than in the increasing population. Since a mother needs support from one of her dominant sisters to remain dominant over her daughter (s) and this ally is more likely to be lacking in a declining population than a growing one, mothers will more often become subordinate to their daughters. Similarly, for a youngster to become dominant over her older sister, she needs another sister and her mother as allies. These are more often alive in a growing than in a declining population, and according to Datta (1992), this explains the consistency of the youngest ascendancy rule in provisioned and expanding groups of rhesus macaques and Japanese macaques and the lower occurrence of outranking older sisters in the declining population of baboons.

A genetic explanation is given to explain the absence of the youngest ascendancy rule in provisioned colonies of Barbary macaques and in a feral colony of Japanese macaques, where allies were present. In Barbary macaques, Prud'homme and Chapais (1993) suggest this difference may be a genetic one because they discovered that unrelated individuals rarely supported a younger sister against her older sister (although they support her against lower-born females). This differs from what is known of rhesus macaques and Japanese macaques.

An ecological cause is suggested for the absence of the youngest ascendancy rule in feral colonies of Japanese macaques (Hill and Okayasu 1995). Due to the wide spatial dispersion during foraging, the frequency of aggression was rare, and, consequently, support was rare too.

Note that apart from species that are weakly nepotistic, there are also those that are clearly non-nepotistic such as Hanuman langurs (Koenig 2000). Furthermore, in nonfemale-bonded species, such as gorillas and chimpanzees, matrilineal dominance does not exist and young females rank according to their age and power.

How can we explain why the matrilineal system evolved in some female-bonded species but not in others? In a comparative study of egalitarian and despotic species of the genus *Macaca*, Thierry (2000) attributes this to differences in degree of despotism. He argues that the matrilineal dominance system is more complete in despotic species due to the higher frequency of support among kin (so that more power differentiation develops between matrilines). He believes that this also implies a lower frequency of acts of support among non-kin and that in egalitarian species support is distributed the opposite way, that is, it is more frequent among non-kin than among kin. Furthermore, he shows that dominance styles are phylogenetically conserved (Thierry et al. 2000). This begs the question of what caused the start of the interspecific differences in degree of nepotism between egalitarian and despotic macaques. According to Chapais (2004), this originates from a difference in the "strength of competition" due to the distribution of food. In the case of clumped food, supporting others will be more advantageous. Thus, a nepotistic system develops in which there is a high frequency of support of both kin and non-kin (in contrast to only kin as suggested by Thierry). When food is dispersed and causes scramble competition, it cannot be monopolized and support becomes less useful (both among kin and among non-kin).

Support: Kin Selection, Reciprocation, and Exchange

Support in fights, or coalition formation, is often thought to be "altruistic" because of the energetic costs and risks of injury to the actor and the benefits to the receiver.

As regards the benefits of receiving support, it increases the likelihood of winning a fight, as larger coalitions beat smaller ones (wedge-capped capuchin monkeys (Robinson 1988), bonnet macaques (Silk 1992a)).

The cost of coalitions is difficult to estimate, but often it is assumed that one partner bears most of the costs while the other reaps the benefits (presenting thus a case of altruism). If so, the theory of kin selection and that of reciprocal altruism are believed to explain these supposedly altruistic acts.

As regards kin selection, in Old World primates, individuals support kin more often than non-kin, e.g., in pigtails (Massey 1977), rhesus (Widdig et al. 2006), Japanese (Chapais et al. 1997), Tonkean (Petit and Thierry 1994), Barbary macaques (Widdig et al. 2000), chacma and yellow baboons (Silk et al. 2004; Walters 1980), and gorillas. Furthermore, individuals aid kin more often if they are more closely related (pig-tailed macaques, chimpanzees, and rhesus monkeys).

In cases of reciprocal altruism, support is supposed to be reciprocated or exchanged for something else. Reciprocation of support is found in a comparative study of rhesus macaques, stump-tailed macaques, and chimpanzees by de Waal and Luttrell (1988). Since the authors statistically partialled out effects of proximity, kinship, and same-sex combination, they argue that reciprocation indicates that individuals keep mental records of the number of acts received from each individual and that they match the number of acts they give to what they have received from each partner, so-called calculated reciprocity. However, in this study, the effects of dominance ranks and grooming behavior are ignored, and data over five consecutive seasons were lumped together. Therefore, what seems to be proof of keeping mental records may have been simply a side effect. Reciprocation appears to be a side effect, for instance, in the long-term study of the same colony of chimpanzees analyzed per season by Hemelrijk and Ek (1991). It involves a sex difference since chimpanzee males reciprocated support whereas females did not. Males, however, only reciprocated support if their hierarchy was stable; if it was unstable, males supported those they groomed (Hemelrijk and Ek 1991). Because of this, and since there was insufficient indication that there was any negotiation for support because individuals did not significantly comply with requests from others (Hemelrijk et al. 1991), it seemed that males might have joined in one another's fights opportunistically in order to attack common rivals. This may have been the cause of the reciprocation among males. Since males may benefit directly from such joint attacks, supporting behavior is selfish (Bercovitch 1988; Noë 1990; Chapais 1996; Prud'homme and Chapais 1996), and there is no need for the participants to keep records.

Also a modeling study confirms the possible occurrence of reciprocation and exchange as a side effect (Hemelrijk and Puga-Gonzalez 2012). The model represents grouping individuals that groom and fight with others nearby. It suggests that reciprocation and interchange emerge as a side effect of proximity. In the model, the spatial position of individuals in the group appears to be relatively stable, and thus individuals interact more frequently with partners that are in proximity than those that are far away. Therefore, they groom, fight, and support each other more frequently which results in the emergence of these patterns (Hemelrijk and Puga-Gonzalez 2012).

As in chimpanzee males, reciprocation of support has been reported in one study of male baboons (Packer 1977) but not in another (Bercovitch 1988). This difference possibly is related to a difference in the stability of the hierarchy (Hemelrijk and Ek 1991).

The sex difference in reciprocation of support is in line with detailed earlier studies by de Waal (1978, 1984), in which he found that coalitions by males were mainly opportunistic and only corresponded with their social bonds during periods in which the position of the alpha-male was clear (de Waal 1984). Female coalitions, however, were more stable and always coincided with their social bonds (Hemelrijk and Ek 1991). Thus, whereas male coalitions seem to serve status competition, female coalitions are directed toward protection of kin and affiliation partners.

Recently, an alternative mechanism to explain reciprocity has been proposed, "emotional bookkeeping" (Schino and Aureli 2009). It suggests that the frequency and quality of previous and present social interactions with a particular partner elicits a specific emotional state. This emotional state may lead to reciprocation and interchange of beneficial acts without relying on high cognitive mechanisms.

Furthermore, de Waal and Luttrell (1988) studied reciprocity of "revenge." By revenge, one means attacking someone while supporting another for the reason that the subject has received similar "contra-support" before. In this study, it was found that revenge is reciprocated only among chimpanzees, not among the two monkey species (i.e., macaques). This is interpreted as if the individuals aim their support against some individual because they have been attacked in a similar way: they have suffered support against themselves. De Waal and Luttrell consider this a sign of a greater cognitive capacity in chimpanzees because chimpanzees keep track not only of acts of support but also of revenge. However, there are three alternative explanations for this pattern. First, the authors lumped together data of five seasons despite changes in dominance ranks and in the stability of the power of the top male. In a study in the same colony, but in an analysis of support data per season, Hemelrijk and Ek (1991) found no reciprocation of revenge. Therefore, the apparent reciprocation of revenge may have resulted from the lumping together of data, and in any case, it is unlikely that individuals keep track of acts of revenge over a period longer than one season. Second, reciprocation of revenge has also been observed in monkeys, e.g., bonnet macaques (Silk 1992a), and also among related female gorillas (Watts 1997), which pleads against the hypothesis of the need of high cognition for such reciprocation. Third, reciprocity of "revenge" emerges in an individual-based model as a side effect of the gradient of the hierarchy (Hemelrijk and Puga-Gonzalez 2012). When the hierarchy is shallow, aggression is known to be bidirectional, because it involves little risks for both partners, and when the hierarchy is steep, aggression is unidirectional (i.e., from dominants to subordinates). In this model, incidental coalitions are observed when, by accident, after a fight between two individuals, a third nearby individual attacks one of the former opponents. Opposition in such incidental coalitions follows automatically the same pattern as dyadic aggression: it is unidirectional when the dominance hierarchy is steep and bidirectional when the dominance hierarchy is shallow. This is statistically recorded as reciprocation of contra-support or opposition but lacks cognitive rules for revenge and for its reciprocation.

Communal Rearing and Allomothering

Usually the mother takes care of the infant alone. In callitrichids (tamarins and marmosets), however, everyone (both parents and mature offspring) assists in rearing the newborns by carrying them and provisioning them. Mature offspring postpone their departure from their natal territory and delay independent breeding (Rapaport 2001). In a number of female-bonded species, youngsters are protected and helped in fights so that they rank immediately below their mothers (matrilineal dominance system, see preceding section), and in all species youngsters are protected in fights that are dangerous. Furthermore, in many species, unrelated individuals may nurse and carry youngsters (allomothering); they cuddle the infant, embrace it, groom, and protect it (McKenna 1979). Allomothers are usually young, nulliparous females, ranking below the mother; often they are sisters of the infant. In this way, the allomother learns how to handle an infant, which increases the chance of survival of her own offspring (Lancaster 1971). An advantage to the mother seems to be the shortening of the interbirth interval (Fairbanks 1990) and the increase of her reproductive success (Ross and MacLarnon 2000). On the basis of detailed comparative studies of macaques, Thierry (2004) argues that two assumptions suffice to explain interspecific variation in degree of allomothering in *Macaca*: (a) attraction to infants and (b) constraints of social structure

(McKenna 1979). First, all females are strongly attracted to all infants. Second, in certain species, mothers protect the infants with greater care than in others, and therefore, in these species, allomothering is counteracted. These species are the species that belong to the two despotic grades of macaques, whose aggression is intense and among whom power differences are great. This may cause problems for females when they have to retrieve their infants. In contrast to this, in egalitarian species, power differences are small and aggression is mild. Thus, differences in the degree of allomothering result from a kind of social epigenesis.

Collective Defense of Home Ranges

Species and groups differ in the way in which they use their home range. Depending on this, fights with other groups may aim at the defense of only one food source (e.g., fruit tree) or of a whole territory (Cheney 1987). A number of species have special intergroup calls that are meant to separate the groups spatially (e.g., in mantled howler, capuchin, mangabey, siamang, yellow-headed titi). Most territorial species, however, have intergroup calls that incite the other group to fight them (e.g., dusky titi, gibbon spp., vervet, colobus).

If actual fights between groups occur, in chimpanzees this may lead to killing an adult of the other group (Wilson and Wrangham 2003; Wilson et al. 2004).

Usually, males are more active than females in fights between groups. In macaques, however, females may also participate. In both sexes, higher-ranking individuals participate more often than lower-ranking ones (Cooper 2004).

Behavior Against Predators

When primates meet a predator, they flee individually (so do large species) or hide (in particular, smaller species). Furthermore, they may protect themselves and their group members in other ways such as (a) by mobbing the predator, (b) by scanning the environment for early discovery of predators, and (c) by warning other group members.

Mobbing predators has been described for baboons, rhesus monkeys, and all three ape species. Each of these species was observed to attack tigers or lions (Cheney and Wrangham 1987). Scanning the environment has been described for a number of primate species such as red-bellied tamarins (Caine 1984) and chacma baboons (Hall 1960). In a series of experiments, tamarins appeared to scan most frequently during the most dangerous periods of the day and in the presence of the most dangerous stimuli. Further, tamarins appeared to divide the duty of scanning among group members. In relation to protection against predators, the spatial distribution of the individuals of the different sex age categories in progressions has also been studied in baboons (Altmann 1979; Rhine and Westland 1981).

Most primates use alarm calls to warn against predators. Such calls are altruistic in the sense that they are harmful to the sender, because it attracts the attention of the predator to the caller, but beneficial to others that are close by. It has been debated whether kin selection is the main evolutionary force behind these calls because it is usually kin that is protected by these calls. However, newly immigrant males also tend to call loudly in spite of the fact that they have no kin members in the group (Cheney and Seyfarth 1981). Many species of primates use different alarm calls for different predators. Such a differentiation is described for vervets, red colobus, Goeldi marmosets, pygmy marmosets, cotton-top tamarins, and gibbons (Cheney and Wrangham 1987; Dugatkin 1997). Vervets emit different calls when the predator is a leopard, an eagle, or a snake (Struhsaker 1976). In playback experiments of the different calls, vervets appeared to respond to leopard alarms by climbing into the trees; at eagle alarms they looked up, and at snake alarms they looked down. Because of the fine distinction between these alarm calls (almost resembling human language), it has been asked whether alarm calling can be considered intentional warning. Evidence points against this, because vervets continue to give alarm calls after everyone in the group has heard them (Cheney and Seyfarth 1985) and because the intensity of these alarm calls and other protective actions by mothers remained similar whether or not their daughters were informed about the presence of the predator (Cheney and Seyfarth 1990).

Conclusion

Cooperation within a group of primates mainly concerns grooming and coalition formation. Sometimes it involves communal hunting, food sharing, and helping to raise young of others and defense against danger from the outside. Such defense involves collective defense of a home range against another group or defense of a group against a predator. The specific patterns of cooperation depend on the social system and the kind of primate involved. Behavioral acts, such as grooming, coalition formation, and tolerance during feeding, have originally been considered as “altruistic” but are presently often considered advantageous for both parties, the actor and receiver. Furthermore, patterns of coalitions and their exchange and patterns of grooming (such as “reconciliation” and “consolation”) have for long been considered to reflect sophisticated cognition, but it is increasingly acknowledged that these patterns may also arise from simple behavioral rules.

Cross-References

- ▶ Evolution of the Primate Brain
- ▶ Great Ape Social Systems
- ▶ Primate Intelligence
- ▶ Primate Life Histories
- ▶ The Hunting Behavior and Carnivory of Wild Chimpanzees
- ▶ Theory of Mind: A Primatological Perspective

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Primate Intelligence

Richard W. Byrne

Contents

Abstract

Brain size has traditionally been employed as a measurable proxy for species intelligence. Using allometric scaling of brain size relative to body size shows the biological cost suffered from investment in brain tissue. Shifts in diet type are the engine permitting increased investment in brain tissue because higher energy diets allow a larger brain at any given body size. Relative brain size, however, confounds effects of gut size required for particular diets with effects of brain size required for enhanced cognitive function. In contrast, the absolute size of brain parts specialized for particular functions gives evidence of the computational power of those systems. Correlational analyses strongly imply that demands of social complexity, rather than difficulties associated with frugivory or embedded foods, led to evolutionary increase in simian primate brain size. Primate brain expansion has largely involved the neocortex, with correlated increases in the cerebellum; among living primates, neocortex size

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R.W. Byrne (✉)
Centre for Social Learning & Cognitive Evolution, School of Psychology & Neuroscience,
University of St Andrews, Scotland, UK
e-mail: rwb@st-andrews.ac.uk

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predicts frequency of use of tactical deception and of innovative responses. These capacities likely rely on extensive memory for social information. Only among great apes is there evidence of understanding how systems work, whether social or technical, and this ape/monkey difference may be mediated by specifically cerebellar expansion. Representational understanding may derive from the ability to parse complex behavior, allowing imitative learning of elaborate new skills.

Introduction

There are three ways in which physical anthropologists might be interested in primate intelligence, corresponding to different theoretical formulations. Firstly, a very widespread view among social scientists is that human intelligence is *unique and indivisible*, shared with no other species (Macphail 1982, 1985). This does not mean "unique, just as each species' intelligence is unique," nor simply "uniquely large," both of which are undeniable; rather, human intelligence is seen as incomparable, and anyone seeking seriously to relate animal and human intelligences is misled. Human intelligence is taken to be a consequence of developing the faculties of language and speech. Thus, on this stance, the key question for human evolution is at what point in human evolution did our makeup change in a way that permitted the development of language. The (unique) origin of intelligence equates to the (unique) origin of language. Replacing a hard question with a famously intractable one leads to no obvious avenue for further research. Moreover, while in the end it may turn out that the gulf between human intelligence and that of any other animal is an unusually large one, to assume a priori that there is no comparison makes good sense only for a creationist. This position will therefore not be considered further.

At the opposite extreme, intelligence has been treated as a continuously varying *quantity*: traditionally called "g" in psychometric psychology, for "general intelligence," or IQ in common parlance. On this view, the evolutionary issue is whether intelligence changed gradually or in steps, and comparative phylogenetic data of primates can be used to pin down when in human evolution such changes occurred (see chapters "▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms," and "▶ Modeling the Past: The Primatological Approach," Vol. 1). Further, by exploring the ecological correlates of intelligence in living primate species, insight can be gained into the current adaptive value (usefulness) of intelligence and thereby reveal clues to its evolutionary origin. What primatology needs to bring to this enterprise is the equivalent of an intelligence test for animals: a fair way of comparing the intellects of living species. This has been the most popular and to date the most productive approach to primate intelligence, but in this chapter, I will suggest that it is only a rough approximation to the truth and may be of limited future value.

Finally, lying between the two extremes of intelligence-as-language and intelligence-as-quantity, intelligence can be treated as a heterogeneous *skill package*:

a mixed bag of devices and processes, endowments, and aptitudes, in fact all those capacities that lead us to label everyday behavior as "intelligent." I will argue that this rather messy vision in fact offers the most promise for the future use of comparative data in understanding the evolution of our most vaunted feature, human intelligence.

Intelligence-as-Quantity

Intelligence as measured within psychology is a matter of differences in ability among people. Strictly speaking, then, intelligence is an individual-level phenomenon. However, over and above the differences in problem-solving ability among humans (and presumably also in other species), individuals share a "common denominator" potential for intelligence by virtue of species membership. It is this genetically based, common denominator that is meant by talking of "differences in intelligence between species." Species differences in intelligence are clearly liable to be much greater than the small differences within human intelligence.

How can *species intelligence* be measured? An obvious starting point is to co-opt and adapt the tools of psychometric psychology: surely measures designed for the small variations in human intelligence will prove sensitive enough for the larger species differences. In practice, this is not as easy as it might seem. One reason is that, although most people consider they can deduce intelligence from everyday behavior, psychologists have preferred to define intelligence operationally, as "what IQ tests measure." As a result, sadly little expertise in psychometrics is available to inform how to infer intelligence from behavior. Still, a considerable battery of tests, broadly comparable to the items of an IQ test, has been applied to animals, using the tools of the animal learning laboratory: Skinner boxes, Wisconsin General Test Apparatus, and so on. Unfortunately, the results have been disappointing, as far as measuring species intelligence goes – and perhaps this should not be a surprise. Human intelligence testing has shown the inappropriateness of grabbing a test, devised in one culture, and using it on people from another culture. The problem is that tests must be calibrated against some other achievement (for human IQ tests, usually educational success), and these measures of achievement are not culture-free; the difficulty is obviously far greater across species. Only a few animals are motivated by rewards similar to those that motivate us, see the world in rather human ways, and interact with the world in a similar way to humans. If researchers rely on human estimation of difficulty in some "behavioral IQ test for animals," they are liable to equate cleverness with similarity to humans. The history of laboratory-based comparative psychology has gone through a series of cycles, with striking species differences in intelligence first claimed and then the difference later discovered to lie rather in perceptual capacity, motivation, or species-typical traits better understood as special-purpose adaptations for particular environmental features (see reviews by Warren 1973; Macphail 1985). Goldfish were once considered less intelligent than rats, because they could not learn visual discrimination tasks – until it was realized that their visual acuity was greater in a downward direction. When tasks were presented on the bottom of the tank, the difference vanished. Among primates, colobines were (and still often are) considered unintelligent compared to cercopithecines – but the latter are frugivorous, readily motivated to perform tasks in return for fruit or other concentrated food. Colobines are folivores, not adapted to compete for (or even able to digest) small items of high-quality food; it is hardly a level playing field. Barn swallows show phenomenal abilities to find their way over great distances to return to the same barn after many months, using the positions of sun and stars, polarized light, and magnetic fields; but they show no other signs of great intelligence, and migratory abilities are not helpfully seen as evidence of intellectual level. Small wonder then that some biologists have doubted whether intelligence is an appropriate measure by which to compare animals at all. Animal adaptations are fascinating, they argue, but calling that intelligence adds nothing to our understanding. Often, psychologists' definitions of intelligence stress the need to deal with environmental challenges: e.g., "the aggregate or global capacity of the individual to act purposefully, think rationally, and to deal effectively with his environment" (Wechsler 1944) or "the faculty of adapting oneself to circumstances" (Binet and Simon 1915). If intelligent for an animal species means "well adapted to the environment," then presumably all species are "intelligent" in their own, nonhuman ways. And while many performances of animals *look* intelligent in the human sense, there is every reason to suppose that their development is under tight genetic guidance.

Surely, however, adaptations specific to solving particular environmental problems should be distinguishable from real intelligence by its quality of *flexibility*, allowing individuals to find their own solutions even to novel problems. Species-typical performances are most likely adaptations (although not all will prove to be: the wearing of bodily adornment or coverings is, after all, species-typical in humans!). But the importance of species-level intelligence is its potential for allowing *individual* flexibility in learning and problem solving. This approach points to the use of observational data of natural behavior to deduce intelligence, just as we do every day among ourselves. However, in examining natural behavior for signs of the individual-level flexibility and creativity that can signal species intelligence, the same danger of confusing genetic adaptations with flexible intelligence occurs as with laboratory testing. An anecdote of my own error may serve as a cautionary tale. Watching border collies herd sheep, I did not doubt the dog's greater intelligence. The sheepdog responds to the whistles of a shepherd with flawless outmaneuvering and controlling of a hundred sheep. Of course, this wonderful performance depends on the innate antipredator reactions of sheep. Bunching and running in tight-packed flocks when attacked makes it difficult for a wolf to single out a potential kill but easy for a sheepdog to maneuver a group. The dog is also equipped with innate tactics, partly as a result of its wolf ancestry and partly as a result of thousands of years of domestication; these tactics can be seen in any untrained sheepdog let out to chase some sheep. But the dog is also able to learn the complex system of whistle signals and is then able to deploy its tactics to order; the sheep, in contrast, are unable to overcome their innate restrictions. My faith in this simple picture was shattered by spending some time with Gujarati shepherds on the Little Rann of Kutch in India. Like British shepherds, they whistle their commands; it seemed a familiar scene. Eventually, I noticed the sheepdogs: asleep. The sheep in Gujarat learn to understand the shepherds' commands and follow them, treating the shepherd as herd leader. The dogs' role is not one of herder but only a source of protection from wolves. Dogs may seem especially intelligent to people because they happen to use facial musculature for visual communication, giving rise to expressions that resemble our own and have similar meanings, and because their forward-facing eyes and long nose make their direction of attention obvious. We can "see" what they are thinking, and recent work shows that domestication has equipped dogs with particular traits that fit into this two-way cooperation (Miklosi et al. 2004). Sheep are foreign to us, because they rely more on olfaction and their facial expressions are relatively cryptic to us, but it is premature to assume them unintelligent.

A proper comparison of intelligence, shown by each of the species relevant to reconstructing human cognitive evolution, is therefore a tall order. Attempts to use general-purpose laboratory tests have often foundered on extraneous differences in natural aptitudes, perceptual capacities, and motivation; in any case, relatively few species are available for detailed examination in captive settings, and comparative phylogenetic analysis depends on using a broad range of species. Yet to accurately attribute differences in natural behavior to intelligence, rather than other evolved aspects of the species biology, requires in-depth study of each species under a range of conditions and so is almost as restricted in what data are available. In consequence, most progress in evaluating animal intelligence as a quantity has been made by using an indirect indication of intelligence, brain size, which can be accurately measured anatomically.

Brain Size as a Measure of Intelligence

The clearest evidence that brain enlargement confers adaptive advantage comes from examining the costs of a large brain: species can tolerate retention of neutral traits, but for a costly organ to evolve necessitates compensating advantages. Brain tissue is metabolically expensive (Aiello and Wheeler 1995). In adulthood, the human brain consumes about 20 % of the basal metabolic rate, and during childhood this percentage rises to 50 %. Moreover, this demand for energy is remorseless: unlike other organs, the energy supply to the brain has to be constant, and irreparable damage results from only a few minutes of interruption. Having a large brain has incurred other disadvantages for us, as well as this energetic drain. At birth, the human child's head is a tight fit in the birth canal compared with the easy passage of other great ape babies (Leutenegger 1982). Birth is consequently a prolonged, often painful, and sometimes dangerous process for mothers; among other great apes, birth takes only a few minutes. Finally, human brains grow for an unusual amount of time, considering their already-large size at birth (Harvey and Clutton-Brock 1985). During this phase of postnatal brain growth, human babies are relatively immature and helpless, so they require years of time-consuming care from the mother or family. Among primates, the only plausible explanation for brain enlargement in the face of such clear costs is an intellectual benefit. To measure species intelligence, then, it should be possible to use brain enlargement. Difficulties arise, however, in deciding the baseline for measuring enlargement.

Larger animals, in general, have larger brains. As the absolute size of living things changes, the relative proportions of their parts are generally found to change. In this case, absolutely larger animals have relatively smaller brains than expected from linearly scaling-up smaller ones (Jerison 1963, 1973). These regular trends have led to the use of allometry to calibrate brain enlargement, against a baseline of the size expected from body weight. In allometric scaling, for a given group of animals, a double logarithmic plot of the parameter at issue is made against body size; provided some sort of power relationship is involved, this forces the species points onto a straight line. For brain size, plotting against body size on logarithmic coordinates gives a reasonably straight line for primates, as for other groups of animals (Passingham 1981). Whether a species lies *above* the line (has a relatively larger brain than expected), *on* the line (has average brain size), or *below* the line (has a relatively small brain) is taken to index its intelligence. For instance, "encephalization quotient" refers to the actual size of a mammal's brain divided by that expected for a typical mammal of its body size (Jerison 1973; see also Clutton-Brock and Harvey 1980). This technique has been used most often in evolutionary analyses of animal intelligence.

However, comparing species in intellectual ability by using their relative brain sizes calibrated with allometric scaling leads to a paradox which brings the whole approach into question. Scaling brain size against body size is implicitly making a strong claim about the functioning of neural tissue. The implication is that an animal with an expected brain size of 2.0 g and a real brain weighing 2.1 g and an animal with an expected brain size of 200 g and a real brain weighing 210 g are "really" equally brainy – even though the latter differs from the expected brain weight by 100 times as much neural tissue as the former. This is a very puzzling result for anyone used to computational (Turing) machines, since these are ultimately limited in power by the number of their elements. The paradox comes from mixing metaphors of what the brain is doing. If the brain is a sort of "on-board computer" (Dawkins 1976) that governs intelligent function, then the *absolute* number of neurons available for computation must be relevant, not the number relative to body size. (The logic here is that neural transmission speed is known to be the same in all mammalian brains, and evolution will have optimized neural programming in each species: thus differences will not reflect relative efficiency or hardware or software, as is the case in most artificial computers.) Bigger brains will be better brains, when it comes to flexible and intelligent responses, regardless of the species' body size. In contrast, using allometric scaling against body size presupposes a more traditional scheme in which animal brains function by making responses to stimuli in a more-or-less reflex manner. The underlying model of the mind is then closer to an automatic telephone exchange than to a computer. Lines from/to subscribers in the telephone system model correspond, in bodies, to sensory and motor neurons. So, input/output connections will determine how big the system to handle them needs minimally to be. Larger bodies need larger brains for these prosaic purposes, and only measuring brain tissue *relative* to body size will show the extent to which processing can be more flexible and intelligent than the minimum. The on-board computer and telephone exchange models cannot both be right – or rather, they will be appropriate for *different* systems within a single brain, and the error is to assume that one or other can be neglected entirely (Byrne 1995b, 1996b). Accepting this more complex view, those brain parts involved in noncomputational body function should increase in size in some regular way with body size, whereas those parts used for computation should not. The *absolute amount of brain tissue free for computation* should give us an idea of the potential intelligence the brain can show, not the amount relative to body size. (Note that it is slightly more complicated than that, as neurons vary in size and packing density across species.) It should be no surprise, then, that allometric analysis of brain size relative to body size and alternative methods that in some way measure absolute sizes produce conflicting results (see Deaner et al. 2000).

Relative Brain Size: The Value of a Brain

Allometric scaling shows that, among mammals, the primate order as a whole is larger brained than most other groups (Jerison 1973). But when strepsirhine primates are partitioned from the rest, they turn out to have brains about the size predicted from mammalian body size (Passingham and Ettlinger 1974). The monkeys and apes, however, have brains twice as large as those of average mammals of their size. What does this mean? Following the arguments of this chapter, disproportionate brain size in relation to body size is not simply a matter of greater intelligence and must be understood in terms of costs as well as benefits. Any species with brain relatively large for its body size inevitably incurs greater risks than a small-brained relative, from the remorseless demand for higher metabolic energy. The relatively large-brained monkeys and apes are thus bearing a much greater cost from their larger brains, on average, than most mammals: how, and why, are these increased costs acceptable?

Primates with home ranges that are large in area tend to have relatively large brains (Clutton-Brock and Harvey 1980), and this has been used to argue that environmental complexity has a powerful influence on primate brain size. But there is an alternative explanation for that correlation: as an artifact of selection for bigger bodies in more folivorous species (Byrne 1996b). Folivory relies on a complex or at least large stomach: for example, the foregut fermentation chamber of colobine monkeys or the large hindgut of gorillas. Leaves are relatively abundant in most primate habitats, so primates with more folivorous diets can find sufficient food for their nutrition in smaller home ranges. By contrast, frugivory requires a larger range area, for year-round access to a variety of fruit species and other sources of nutrients, but the high sugar content allows digestion by a shorter gut. Other things being equal, primates that eat more fruit will have smaller bodies and larger home ranges than those that eat more leaves, causing a correlation between

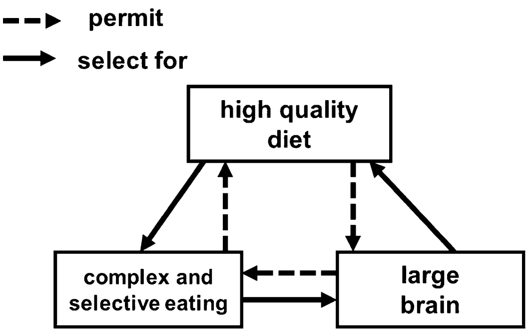

Fig. 1 Brain size and diet. Schematic illustration of the relationships for primates among diet quality, brain encephalization (i.e., size in relation to body size), and the cognitive skills required to find and process foods. Note that specialization in *low-quality food/cognitively undemanding/relatively small brain* is just as effective as an evolutionary strategy as *high-quality food/cognitively demanding/relatively large brain*

frugivory and relative brain size, regardless of any differences in intelligence. Variations in brain size relative to body size may therefore be a side effect of differences in body size due to diet type rather than a direct result of selection for larger brain size.

Since gut tissue is metabolically as costly as brain tissue, and diets requiring only small guts (frugivory, meat eating) often provide a surplus of energy by the time a nutritional balance is obtained, primates with small guts are on the whole likely to be better able to “afford” larger brains (Aiello and Wheeler 1995). Clearly, the grade shift toward meat-based diets in the later hominins might be related to the massive brain expansion in these species. The relationship between energy supply and the size of brain that can be afforded for a given body size does not, however, explain why larger brains should have evolved in some taxa and not others: the opposite is just as feasible, a trend toward smaller brains in species with less need for high-quality diets (see Fig. 1). Moreover, the fact that the energy demands of the brain are constant suggests that the large brain/high-energy diet is a particularly risky evolutionary strategy for which a compelling competitive advantage must exist.

One possibility is that a niche for a high-quality diet specialist may happen to become available, and the survival cost of large brain size is thereby lessened for any species that exploits that opportunity, resulting in a new equilibrium at a higher relative brain size. However, higher quality diets are usually based on sparse, hard-to-find, hard-to-access, or hard-to-process foods (e.g., fruit, nuts, meat), so this is not entirely plausible. More often, the causal chain is likely to run in the opposite direction: from a real need for higher intelligence, precisely in order to exploit a new, high-quality food supply. It might even sometimes be the case that ecological pressures for greater intelligence – and thus a larger brain – drive selection for a larger body, in order to support it. The frequently noted trend over geologic time for species of the same taxa to increase in size might sometimes be a consequence of an arms race of intellectual competition, selecting for larger brains and consequently larger bodies to support them at the same level of survival risk, coevolving with changes in diet.

Absolute Brain Size: The Power of a Brain

To measure the computational power of a brain, it will be necessary to estimate the absolute number of neurons available for flexible, problem-solving purposes: the lack of any overwhelming correlation between overall brain size and observed smartness in animals suggests that simply using the total brain volume will not do. Jerison (1973) was well aware of the need and developed an index of "extra neurons" by calculating the absolute number of neurons beyond what was minimally necessary for bodily function. With a similar aim, Bauchot and Stephan (1966) attempted to identify the taxonomic group with least intelligence, as a baseline from which all others deviated. However, difficulties in deciding what volume of neural tissue is minimally necessary, or whether any species entirely lacks flexible intelligence, have prevented general adoption of these approaches. In recent years, the same problem has generally been tackled in a different way by comparing the volume of one part of the brain, the neocortex, against the rest. There are two assumptions involved here. First, that the primate brain has undergone mosaic evolution, with some parts growing in size and power at the expense of others, for a given overall size (Barton 1998; Barton and Harvey 2000). On a broad scale, this assumption is hard to doubt: for instance, haplorhine primate brains are clearly more dominated by visual cortex and less by olfactory lobes than those of most other mammals, including strepsirhines. The second assumption is that a primary function can be safely assigned to expansions of particular regions – in particular, that the neocortex is involved in abstraction, thinking, and executive functions such as effective problem solving. This is supported by a long history of deducing brain function from task failures after accidentally or deliberately inflicted lesions, somewhat problematic to interpret but consistent in pattern, and more recently supplemented by the differences in patterns of energy use revealed by brain imaging. (Note, however, that most published brain images conveniently omit the "lower" cerebellum: I return to the role of the cerebellum later in the chapter.) More pragmatically, it can be noted that the increase in brain volume in the primates over that of other mammal groups is chiefly due to neocortical enlargement; and among primates, it is the neocortex that varies most strikingly between species, with correlated changes in cerebellum (Whiting and Barton 2003), whereas the rest of the brain shows much less evolutionary change. This implies a strong selection pressure for neocortical enlargement in primates, and an intellectual function is the only serious candidate for this selection pressure.

If it is taken, then, that primate neocortical enlargement measures specialization in some sort of intelligence, can ecological correlates indicate the function it subserves? Sawaguchi and Kudo (1990) found that the neocortex was larger in species living in bigger social groups, both in strepsirhines and in frugivorous platyrrhines. Also, in frugivorous haplorhines, polygynous species (one male living with more than one female) had larger neocortices than monogamous species. These findings hint at a social origin of intelligence (Jolly 1966; Humphrey 1976; Byrne and Whiten 1988), and Dunbar (1992, 1995, 1998) has gone further to support this idea, examining whether neocortex size correlates with measures of social or environmental complexity in living primates. He used both raw neocortical volume and several more complex functions; all gave similar trends but *neocortex ratio* (ratio of neocortex size to that of the rest of the brain) gave the clearest effects. Measures of environmental complexity – range area, day journey length, and the amount of fruit in the diet – were found to be unrelated to neocortex ratio when body size effects were removed. In contrast, average species group size correlated with measures of neocortical enlargement, supporting a predominantly social function of primate intellect. Dunbar proposes specifically that neocortical size limits the social complexity that an individual can cope with: social complexity increases with group size, so groups begin to fragment when their size increases past a complexity limit set by neocortical size. These analyses can be criticized on statistical grounds – for instance, neocortical ratio is correlated with body size, and using species as data points brings problems of phylogenetic independence – but the broad findings have been confirmed, using absolute neocortex volume and the volume of the rest of the brain as independent predictors and the method of independent contrasts to avoid phylogenetic bias (Barton 1996; Barton and Dunbar 1997; Barton and Harvey 2000). Neocortical expansion is clearly linked with increased social group size in primates (and indeed also in bats, carnivores, and cetaceans).

These correlations give little clue, however, as to precisely what social skills are possible, or enhanced, by the possession of a larger neocortex. The problem is, of course, the difficulty of finding a species-fair and widely applicable measure of social skill, but there are now some steps in this direction. The most detailed analyses so far have been applied to the use of deception by primates within their own social group. Social manipulation of affiliated conspecifics, avoiding the disruptive use of violence, lies at the heart of the Machiavellian intelligence hypothesis (Humphrey 1976; Byrne and Whiten 1988). Cases where an individual achieves its ends by successfully deceiving another have long fascinated primatologists (Goodall 1971; de Waal 1982, 1986; Byrne and Whiten 1985), which made it possible to assemble an extensive corpus of carefully documented records, spanning all major groups of primates (Byrne and Whiten 1990). Preliminary analyses showed that most acts of deception were carried out with little sign of intentional understanding but nevertheless served effectively to manipulate the visual attention of other individuals and thence their understanding of the situations (Whiten and Byrne 1988a, b). These visual perspective-taking abilities were confirmed experimentally, in chimpanzees, when researchers modified naturally occurring situations of food competition for laboratory testing (Hare et al. 2000, 2001); the field data indicates, however, that visual perspective taking is widespread also in monkeys. A larger corpus confirmed that only in the great apes did any of the accounts seem most parsimoniously explained as a result of mental state attribution

(Byrne and Whiten 1991, 1992); even in these cases, alternative, nonmentalistic possibilities are entirely possible (Byrne 1993; Povinelli and Vonk 2003). However, the frequency of use of deception was clearly not uniform across species, nor easily explained as a result of observer effort (Byrne and Whiten 1992). Byrne and Corp (2004) investigated whether neocortical specialization was involved. Correcting the raw frequencies of observed deception for observer effort by using the number of long-term field studies of habituated individuals over the period, and using independent contrasts to correct for phylogenetic bias, they found that neocortical enlargement – whether measured by neocortex ratio or absolute volume – strongly predicted the rate of use of deception. In contrast, neither the volume of the rest of the brain nor even the species' average group size had significant effects (note that the number of species for which data were available was smaller than in Dunbar and Barton's analyses of group size, so the difference may relate to statistical power). It seems that the use of deception for social manipulation critically depends on neocortex size.

What cognitive processes are likely to be involved in using deception? Given the lack, in the vast majority of cases, of any sign of intentionally planned deceit (Byrne and Whiten 1992; Byrne 1997a), the main attribute would seem to be rapid memory in social contexts: memory of who was present on which occasion, who did what to whom, and so forth (Byrne 1996a). This suggestion finds support from the finding that social grooming is correlated with group size in Old World primate species (Dunbar 1993): for grooming to be valuable as a social currency, a good memory of grooming debts to and from social companions is essential. Innovation of novelty has been shown, similarly, to vary with neocortical enlargement in primates (Reader and Laland 2001). It is less clear what may be minimally needed for the ability to innovate successfully, but an analysis of the innovations employed in primate deception found that most cases involved only generalization of familiar behavior to slightly novel contexts (Byrne 2003b).

The Intelligence to Understand the World

Learning and memory are certainly critical aspects of intelligence to the extent that they allow efficient, rapid, and flexible performance. But there is more to human intelligence than quick learning and reliable memory: to quote one definition, "grasping the essentials in a situation and responding appropriately to them" (Heim 1970). Putting this in more cognitive terms, intelligence implies the ability to *represent* the processes, social or physical, which are going on around us, and to use those mental representations to plan actions that may later be put into effect. Can evidence from living primates be used to deduce when, and in which ancestral species, this sort of intelligence evolved? Getting evidence of such capacities without using the medium of language is tricky, but this is a topic of extensive current research and some progress has been made. With very few exceptions, the evidence comes from great apes, although the interpretation of negative evidence is always problematic. Outside the great ape clade, it is very possible that primate behavior is not based on representational, mental models; even for great apes, interpretations remain controversial and are likely to change both as a result of improved data and sharper theoretical analyses.

Signs of *social understanding*, which include some level of theory of mind ability, have long been reported from analyses of observational data; these have included empathy and sympathy, intentional deception, and pedagogical teaching (de Waal 1982; Boesch 1991; Byrne and Whiten 1991). Until recently, however, the consensus of laboratory experimentation was that great apes entirely lacked any such ability (Povinelli and Eddy 1996; Tomasello and Call 1997; Heyes 1998; Tomasello 1998). However, a number of experimental results have now brought the experimental and observational data sets into closer alignment (for reviews, see Call 2001 and Tomasello et al. 2003): using more naturalistic paradigms to examine great ape problem solving, a series of experiments have shown aspects of intentional understanding. These capacities closely match those apparent in some of the most complex cases of great ape deception, mentioned above (see Byrne and Whiten 1991): the ability to respond appropriately to differences in intention (e.g., accidental versus deliberate, inability versus unwillingness), visual perspective (hidden to a competitor but in view to self, partial versus completely hidden), and other individuals' knowledge (e.g., known to one competitor but not another).

Signs of *technical understanding* have long been claimed for apes, because of the evidence of tool use and tool manufacture in the chimpanzee (and one population of orangutan), but there has been little attempt to work out exactly what understanding is needed for these skills to be learnt (Seed and Byrne 2010). Many animals use detached objects as tools (Beck 1980), the process of tool manufacture is usually quite simple (McGrew 1992), and the strongest argument that great ape tool use relies on representational understanding is that sometimes tools are prepared or selected in advance, out of sight of the place of use (Byrne 1998; Byrne et al. 2013). Most studies of chimpanzee tool use emphasize product rather than process, and in fact the evidence for unusual abilities in manual skill learning is stronger for the case of plant processing than tool use (Byrne 2004). Circumventing the physical defenses of herbivorous plants leads to the use of complex processing (Corp and Byrne 2002a), and both mountain gorillas and chimpanzees have been found to employ hierarchically organized procedures consisting of several modules employed in series or as subroutines (Byrne 1999b; Byrne and Byrne 1993; Byrne and Russon 1998; Byrne et al. 2001; Stokes and Byrne 2001; Corp and Byrne 2002b).

Learning by imitation links social and technical intelligence: by means of social learning, technical skills are acquired. Imitation, in the rich sense of learning new, useful behavioral routines directly from observation, is often thought to rely on prior understanding of mental entities, e.g., "the child must imaginatively place herself in the circumstances of the adult and determine what is the *purpose* of the behavior and *how one goes about* accomplishing that purpose" (Tomasello et al. 1993; my italics). Acquisition of novel behavioral routines by observation has been strongly argued for mountain gorillas, orangutans, and chimpanzees

(Russon and Galdikas 1993; Byrne and Russon 1998; Byrne 1999a, b, 2002; Byrne and Stokes 2002; Lonsdorf et al. 2004), variously on the basis of (a) resemblance in fine detail between behavior of mother and offspring, (b) the fact that disabled individuals learn group-typical manual processes rather than devising more efficient, idiosyncratic versions, and (c) the sheer improbability of highly specific and complex organizations of behavior developing so similarly in each individual without some learning by imitation. It is also usually presumed that the site-specific differences in chimpanzee behavior reflect socially learned traditions in which useful skills are passed on by imitative learning of the critical aspects of processes which are hard for any individual to discover on any reasonable timescale, simple "cultures" (Whiten et al. 1999; Whiten 2000; but see Byrne et al. 2004, Laland and Janik 2006, for caveats).

A tidy picture is thereby painted of great apes – and perhaps only great apes – able to understand other individuals' behavior in terms of intentional properties, giving them the ability to learn novel technical procedures from watching others who already have skills, leading to the elaborate, group-specific traditions in skills of significant technical sophistication described in wild chimpanzees. Given the close relationship of chimpanzees to ourselves, these similarities to human intelligence would be interpreted as resulting from common descent from a shared Miocene ancestor, having the ability to mentally represent intentional and causal-functional aspects of complex processes.

This picture may not be all it seems, however. Over just the same 20-year period in which evidence of richly complex behavior in great apes, once dismissed by experimentalists, has become hard to doubt, a number of theoretical analyses have begun to question what the evidence implies about the mental processes involved. It is important to stress that this challenge is not a reworking of early behaviorist critiques; behaviorism was hamstrung by its insistence on not postulating mental processes as "intervening variables," whereas that is no longer at issue. However, if great apes were equipped with powerful systems for detecting and extracting patterns of statistical regularity in the world around them – patterns that *correspond to* intentions, plans, and cause-and-effect relationships – such use of statistical regularities might be sufficient to explain what the apes do, without their having concepts that correspond to human ideas of mental states and causal relationships. Those may all be dependent on language and function in other ways than as primary causes of behavior.

Consider the case of imitation. There is a body of evidence, sketched above, that suggests great apes are able to learn by imitation the organizational structures of complex skills: how actions are grouped into often-used modules, how modules may be incorporated as subroutines into an overall plan (and thus repeated or omitted, depending on particular conditions of a given task), how sequential ordering affects outcomes, and so on. This is called program-level imitation (Byrne and Byrne 1993; Byrne 1995b; Byrne and Russon 1998) and involves the use of hierarchical organization to structure novel actions. But where do the programs come from: is it essential to discern the demonstrator's intentions, and the cause-effect of how actions achieve their results, to derive a useful program? Not necessarily: if a sufficiently large corpus of behavior can be observed, then recurring patterns among the natural variability of behavior can in principle reveal all the organization underlying skilled action that is necessary for program-level imitation (Byrne 1999a, 2002): “imitation without intentionality” is a real possibility. The process of extracting statistical regularities from the messiness of natural, goal-directed action has been termed *behavior parsing* (Byrne 2003a) and serves to reveal the underlying deep structure of behavior, but it does not depend on explicit representation of intentions and causes. Instead, the extracted structures of behavior link prior circumstances to resulting outcomes, so that if a particular outcome is desired, then those circumstances can be sought and that structure of behavior applied (see also Byrne 1995a, b).

In principle, it is possible that behavior parsing might also underwrite other behavioral routines that appear to rely on understanding ignorance, knowledge, intentions, and dispositions of others. While nothing so specific as for imitation has been worked out to date, Povinelli and Vonk (2003) point out that claimed mental processes of chimpanzees are “suspiciously similar” to those of humans and suggest that this may be because humans (alone) construe behavior in those terms. The implication is that the cognitive system of nonhuman great apes is adept at extracting and using complex patterns of behavioral action but does not represent these patterns in the form of attributions about the mental states of others.

None of these critics suggest that humans *lack* the powerful mental processes for extracting statistical regularities from behavioral observations: indeed, even 8-month-old infants are able to extract statistical regularities from spoken strings of letters, after only a few hours of exposure to monotonously spoken letter strings built according to particular rules (Saffran et al. 1996). And the area of the brain most closely associated with development of patterned motor behavior (Marr 1969), the cerebellum, is especially enlarged in humans, even as compared to other great apes and greatly more than in monkeys (Barton 2012). The point is rather that the way we describe behavior in everyday talk, in terms of goals, plans, and intentions, may be uniquely human. Mention of “everyday talk” may give the clue to the function of intentional-causal representation: rather than primary cause of behavior, such representations may be valuable because they allow pedagogy, explanation, and deliberate retrospective misrepresentation of behavior, using the medium of spoken language (Byrne 2006). Heretical as it may sound, it is worth questioning whether much everyday human behavior relies on intentional-causal analyses of situations: the alternative is that the same, powerful mechanisms for automatically extracting and using statistical regularities (regularities that themselves result, of course, from underlying intentions and causal dependencies) allow us to function in a “fast and mindless” fashion, responding appropriately and efficiently without deep thought about underlying mechanisms (and see Bargh and Chartrand 1999). Perhaps only when in contemplative mood, when asked directly or when trying to explain (away) our actions, do we invoke the machinery of causal-intentional representation.

Conclusion

People often speak as if intelligence were unitary, as if it could be measured on a single scale, but that is perhaps unlikely. If it is accepted that intelligence is not a single "thing" but rather a mixed bag of devices and processes, endowments, and aptitudes that together produce behavior we see as "intelligent," then it makes sense to study separate facets of intelligence independently of each other. Modern psychometric work, following Rozin (1976), recognizes several "intelligences": social-empathic, technical-mathematical, and commonsense-practical (Sternberg and Kaufman 2002). Presumably, in comparing across species, the different types of intelligence are likely to be even more sharply defined, and many cognitive capacities may need to be distinguished – each of them contributing to an impression of intelligent action but originating in different evolutionary circumstances and often at different periods of evolutionary history. Taking that line, it is possible to summarize what is currently most likely to have happened over the evolutionary timescale that we share with living primates.

Primate evolution has seen two separate changes in intellectual potential, with concomitant brain changes. In the first, well-accepted, evolutionary event, selective pressures to cope with and succeed within larger social groups led to a greater ability to learn in social situations, resulting in species with enhanced abilities in social perception (including sophisticated visual recognition of identity and demeanor) and memory (including subtle correlates of past events). This intellectual change was permitted by increased neocortical capacity, with correlated cerebellar enlargement, and gave the ability to learn impressive-seeming tactics of behavior such as deception and cooperation. Deep understanding of the mechanism of these social tactics was lacking in the individuals of these species themselves, and they (like modern monkeys) were not able to imitate novel skills or show insight into causal relationships in the physical sphere.

In the second evolutionary event, ancestral great apes acquired extra abilities. The selective pressure that resulted in this change may indeed have been competition from Old World monkeys, species that now compete with apes for food in almost all their habitats and have clear advantages in terms of more efficient long-range locomotion and digestion (Byrne 1997b). The result was a clade of modern great apes, all of which have "special" abilities valuable for food acquisition, based on their ability to learn novel routines of skilled, bimanually coordinated manual action, sometimes involving tool use, sometimes involving locomotion, and reliant on imitation by behavior parsing as well as exploration. This intellectual change was permitted by an increase in cerebellum size, going beyond that expected from the already large brains of animals much larger than monkeys. Behavior parsing gave these apes a rudimentary ability to understand the *intentions* (as physically attainable goals) of other individuals and a rudimentary ability to understand the *causal logic* (as correlational likelihood) of physical events.

For individuals to go beyond this "behavioral approximation" of intentions and causality, to a deeper understanding of theory of mind and cause and effect, may have required representation of propositions for which there is no evidence in living nonhuman species – and it may indeed have required language. Comparative psychology cannot help, in that case, since the necessary adaptations must be uniquely human. On the other hand, widening the scope of comparative analysis beyond the nonhuman primates, to examine other taxa entirely, offers the prospect of a more general understanding of the evolution of intelligence. Already a promising start has been made, with some cognitively sophisticated species: parrots (Pepperberg 1999), cetaceans (Herman 1986; Rendell and Whitehead 2001), pigs (Held et al. 2000, 2001, 2002), canids (Miklosi et al. 2004), elephants (Bates et al. 2008; Plotnik et al. 2011; Smet and Byrne 2013), corvids (Emery and Clayton 2004; Dally et al. 2010), and tortoises (Wilkinson and Bugnyar 2012). With converging evidence from all these taxa, and a solid body of data on a significant range of nonhuman primates, it will be time to attack once more the persisting problems of studying intelligence: How many kinds of intelligence are there? To what extent are different intellectual capacities localized in the brain? What adaptive pressures select for particular abilities? And so on.

Cross-References

- ▶ Modeling the Past: The Primatological Approach
- ▶ Molecular Evidence on Primate Origins and Evolution
- ▶ Origin of Modern Humans
- ▶ Theory of Mind: A Primatological Perspective
- ▶ The Evolution of Speech and Language
- ▶ The Evolution of the Hominid Brain

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Theory of Mind: A Primatological Perspective

Juliane Kaminski

Contents

Abstract

Human social cognition is unique because humans can, in some situations, make predictions about others' mental states, an ability referred to as "Theory of Mind." Whether other primates also have the ability to attribute mental states to others is a highly debated question. While members of different primate species seem to follow other individuals' gazes and are sensitive to others' attentional states, there is as yet evidence in only a few species for an understanding of others' visual perspectives, knowledge states, or intentions. The hallmark of mental state attribution, false belief understanding, appears to be a uniquely human skill. At present there is no evidence that any animal species understands that others' beliefs can contradict reality, and therefore be false. This is why the consensus is, for now, that although certain primate species understand certain psychological states in others, there is not sufficient evidence

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J. Kaminski (✉)
Department of Psychology, University of Portsmouth, Portsmouth, UK
e-mail: Juliane.kaminski@port.ac.uk

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for true mental state attribution. It remains to be seen whether this view continues to be supported by future studies; in other areas of comparative cognitive science, new results led to dramatic paradigm shifts in recent years.

Introduction

Human social cognition is unique. Like no other species, humans can make predictions about others' mental states – that is, others' intentions, desires, beliefs, and so forth. This ability is referred to as "Theory of Mind" (ToM), a term first introduced by Premack and Woodruff (1978) in their seminal paper asking the question "Does the chimpanzee have a Theory of Mind?" It is called a "theory" because mental states are not directly observable and therefore need to be inferred. Humans develop an understanding of others' psychological states relatively early in life. Children start following others' gaze direction and tracking others' line of sight during their first year (D'Entremont et al. 1997; Moll and Tomasello 2004; Scaife and Bruner 1975). They also seem to understand the function of the eyes while doing so: an infant can distinguish situations during which an observed person's eyes are open and she is therefore able to see from situations during which the observed person's eyes are closed (Brooks and Meltzoff 2002; Butterworth and Jarrett 1991; Lempers 1979; Tomasello et al. 2007). Similarly, around this age already, children understand when others' line of sight is blocked, e.g., by a barrier hiding an object (Moll and Tomasello 2004). Later in life, at around 2 years of age, children start to also understand others' past visual access, namely what they have and have not seen (Dunham et al. 2000; Moll and Tomasello 2007; O'Neill 1996; Tomasello and Haberl 2003), suggesting that the latter ability is cognitively more demanding (Wellman and Liu 2004). It is also by that time that children appreciate that others have desires that can deviate from their own (Rakoczy et al.2007).

However, ToM understanding is only considered to be ontogenetically full-fledged once children understand that others can have false beliefs, a stage which children in Western cultures normally reach around 3.5 years of age (Wellman et al. 2001). Understanding that others have a false belief requires for the individual to understand that another individual's mental state contradicts their own and reality. Therefore, understanding that others have false beliefs requires a fully representational ToM (Wellman et al. 2001), which is why ToM development is considered to be the benchmark for the capability to attribute mental states to others. The standard test for false belief understanding is called the Sally-Anne test (Wimmer and Perner 1983). In this type of test, participants are presented with a hypothetical or re-enacted scenario in which two characters, "Sally" and "Anne," interact over a set of two containers. In the original version, Sally has a basket and Anne has a box. Participants now witness, or listen to, a description of a simple scene in which Sally puts a marble in her basket and then leaves the room. While Sally is away and cannot watch, Anne takes the marble out of Sally's basket and puts it into her own box. Sally then returns and the children are asked where they think she will look for her marble. Children are said to "pass" the test if they understand that Sally will most likely look inside *her* basket first, before realizing that the marble isn't there but in Anne's box.

One question is to what extent these abilities are unique to humans – whether there are any facets of them that we share with other members of our phylogenetic family, the primates. Social cognitive skills would be beneficial to have for many social species, as the social environment often changes rapidly and the individual needs to draw on flexible cognitive skills to adapt to these ongoing changes. The social intelligence hypothesis, formulated by Humphrey (1976), states that social cognitive skills evolved in particular for life in complex social environments, because they help the individual to maneuver freely and adapt flexibly to the constantly changing social environment. The Machiavellian intelligence hypothesis formulated later by Whiten and Byrne (1988) adds competition as a major driving force to this scenario. This hypothesis claims that social cognitive skills evolved mainly to outwit potential competitors in the battle for resources such as food and potential mates. Both hypotheses suggest that we should find social cognitive skills in other species besides humans. To what extent the predicted shared skills would involve an understanding of others' mental states, and could therefore be called ToM, is a very interesting open question.

Gaze Following Behavior in Primates

One of the most basic social cognitive skills is gaze following. Following other individuals' gaze puts the individual in position to gather information about certain aspects of the environment, such as the location of food or predators. This is what makes gaze following a beneficial skill for group-living animals generally. Many primate species follow their conspecifics' or a human's gaze towards outside entities (Povinelli and Eddy 1997; Tomasello et al. 1998).

In a study conducted by Bräuer et al. (2005) with all species of great apes (chimpanzees [*Pan troglodytes*], bonobos [*Pan paniscus*], gorillas [*Gorilla gorilla*], and orangutans [*Pongo abelii*]), a human sat opposite the ape, feeding the subject with food. Then, at a predetermined time during the trial, the human stopped feeding and looked up at the ceiling as if there was something interesting to see there. All great ape species followed the human's gaze by looking up also. This was then compared to a control condition during which the human also stopped the feeding but did not look up, instead looking directly at the wall opposite her. The apes did not look up either in this condition, clearly showing that it was the human's gaze shift which had made them look up in the earlier condition (Bräuer et al. 2005).

There is also evidence that different monkey species, Old World and New World, as well as lemurs, follow the gaze of others (e.g., Burkart and Heschl 2006; Ruiz et al. 2009; Sandel et al. 2011; Tomasello et al. 1998; for a review see Rosati and Hare 2009). Researchers today assume that gaze following is widespread among primates and certain other mammalian species. But whether the ability to follow others' gaze involves an understanding of others' line of sight and perspective and therefore others' psychological state, or whether it is a comparatively automatic response to seeing another individual's gaze shifting in a certain direction, is not possible to determine using this paradigm alone.

This is why researchers designed another paradigm to test if primates also follow the gaze of other individuals around a barrier and therefore geometrically (Tomasello et al. 1999). In this paradigm, instead of looking up at the ceiling, the human looks at a location out of the subject's current view – for example, one side of an opaque barrier which the subject cannot currently see. If subjects just followed another individual's gaze automatically, they would merely shift their gaze in the same direction as the other individual, resulting in them looking at, in this example, their side of the barrier. If, on the other hand, subjects understand something about the other individual's line of sight, they should be motivated to follow the human's gaze to the specific location that the human is looking at. In order to do so, they have to move around the barrier, such that they can see everything from the same angle as the human. Great apes follow a human's gaze around a barrier even if they have to move a certain distance in order to do so (Bräuer et al. 2005). There is also evidence that some monkey species – e.g., common marmosets (*Callithrix jacchus*), Geoffroy's spider monkeys (*Ateles geoffroyi*), and capuchin monkeys (*Cebus apella*) – are able to follow the gaze of others geometrically, indicating that these species, like the apes, do not just automatically react to the gaze shift of others, but actually track the other individual's line of sight, presumedly because they understand another individual's perspective as being different from their own (Amici et al. 2009; Burkart and Heschl 2006).

Another interesting behavior during gaze following experiments, which was first observed in chimpanzees, is so-called "checking back" behavior (Call et al. 1998). The chimpanzees check back, looking again at the human's face, when they have not seen anything interesting after following the human's gaze (Bräuer et al. 2005; Call et al. 1998). Researchers take that as another indication that chimpanzees really do understand the human's perspective in this setting and that they want to confirm the human's line of sight after not being able to see what the human was seeing. Interestingly, there seem to be species differences regarding checking back behavior. While this behavior seems to be robustly present in all the great apes, it is absent in the small ape, i.e., the gibbons. Liebal and Kaminski (2012) examined four different species of gibbons (*Hylobates pileatus*, *H. moloch*, *H. lar*, and *Symphalangus syndactylus*) for their ability to follow the gaze of a human. While the subjects clearly followed the human's gaze, there was no evidence for checking back behavior, indicating that probably the gibbons' gaze following did not include an understanding of the other individual's perspective (Liebal and Kaminski 2012). The same was true for spider and capuchin monkeys, which also follow another individual's gaze, but do not check back after not finding anything interesting (Amici et al. 2009).

To further investigate what primates understand about other individuals' psychological states, researchers have also looked at primates' understanding of the function of the eyes and primates' general understanding of attentional states in others.

Primates' Understanding of Others' Attention

There is much evidence to suggest that various primate species attend to others' attention. All four of the great ape species alter their gestural communication based on the addressed individual's attentional state (Cantero et al. 2001; Kaminski et al. 2004; Leavens et al. 2004; Povinelli and Eddy 1996; Tempelmann et al. 2011). The apes produce more visual gestures, such as reaching, when the recipient of the gesture is in their visual field (Kaminski et al. 2004; Liebal et al. 2004) and produce more tactile gestures, such as touching, when the recipient is not (Liebal et al. 2004). When begging for food from a human, great apes produce visual gestures at a higher frequency when the human's face is oriented (Hostetter et al. 2007) towards them than when it is oriented away, or when the human is bodily oriented towards them rather than oriented away (Call and Tomasello 1994; Kaminski et al. 2004; Povinelli and Eddy 1996; Tempelmann et al. 2011). Chimpanzees seem to attend to the status of the eyes specifically, with studies showing that chimpanzees produce more visual gestures when the human's eyes are visible than when they are not. Chimpanzees also produce more vocalizations when the human's eyes are closed than when they are open (Hostetter et al. 2007). For the other great apes the evidence to date suggests that they may not attend to the status of the eyes specifically, but only to the overall orientation of the face (Kaminski et al. 2004). However, this difference could also be due to a smaller sample size in the relevant studies with other great apes, compared to the studies with chimpanzees.

Different monkey species also attend to others' attentional states. In one study, rhesus macaques preferentially begged from a person whose eyes were oriented towards them, rather than from a person whose eyes were oriented away or covered with a barrier (Flombaum and Santos 2005). Maille et al. (2012) worked with another Old World monkey species, the red-capped mangabeys (*Cercocebus torquatus*). The monkeys in this study also attended to the human's body orientation and begged at higher frequency when the human was oriented towards them rather than away from them. Interestingly, the mangabeys ignored the more subtle cues, like the status of the eyes (Maille et al. 2012). In contrast, capuchin monkeys, which are New World monkeys, seem to be very attentive to others' attentional states, including the status of the eyes. In one study, capuchins looked at a human's face longer when the human looked at them, compared to when the human looked at the ceiling; they also looked at the human's face longer when the human's eyes were open rather than closed (Hattori et al. 2007). There is also evidence for a lemur species attending to others' attention. In a study involving a competitive situation over food, ring-tailed lemurs (*Lemur catta*) avoided food that the human was facing, preferring food that the experimenter was not facing (Sandel et al. 2011). Interestingly, other lemur species tested in the same study did not show the same sensitivity to the human's attention. The authors attribute this difference to the fact that ring-tailed lemurs live in groups with a notably more complex social structure than the other species, supporting the so-called social intelligence hypothesis, mentioned above, which states that social cognitive skills evolved to maneuver in more complex social environments (Humphrey 1976).

Primates' Understanding of Others' Visual Perspective

One way of testing whether primates, like humans, understand others' visual perspective is to confront them with a situation during which they need to assess another individual's visual access to, say, a certain location, in order to achieve their goal. In Flavel's et al. (1978) terminology, an individual proves to have "Level 1 perspective taking" if it understands that another individual's line of sight is blocked by, e.g., a barrier (Flavell et al. 1978). Povinelli and Eddy (1996) tested chimpanzees' understanding of others' visual perspective by confronting them with a situation during which the chimpanzees had to decide which of two humans to beg from. Both humans were holding a piece of food (e.g., an apple); one of them could always see the chimpanzees, whereas the other individual's visual access was blocked – say, by a bucket this person was wearing over the head. (The human who had visual access was also holding a bucket, but held it placed on his shoulder so that it would not block his view.) The chimpanzees in this setting begged from both people indiscriminately and therefore did not seem to attend to whether the humans' visual access to their communicative attempts was blocked or not. In recent years, however, researchers have argued for a paradigm shift that would change the interpretation of this experiment. The revised view is that chimpanzees' cognitive skills might have evolved in the context of competition over resources, rather than to aid more cooperative interactions. This is why researchers now argue that it is more natural for chimpanzees to compete over food rather than to expect another individual to behave cooperatively towards them.

To obtain data that might clarify the situation, Hare et al. (2000) designed a situation during which two chimpanzees, one dominant over the other, compete over two pieces of food. While both pieces are visible to the subordinate animal, only one piece of food is visible to the dominant animal, whereas the other piece is hidden by an opaque barrier from the dominant individual's view. To rule out that the subordinate chimpanzee would simply orient his behavior towards the behavior of the dominant, the subordinate chimpanzee got a head start while the dominant's door was still closed. Once the subordinate had clearly made a choice, the dominant's door was opened and she could enter the arena. The subordinate chimpanzees in this situation clearly preferred to approach the food piece hidden from the dominant to the food piece that both of them had visual access to. To rule out that the subordinate chimpanzees were just seeking to be protected from the dominant individual by the physical barrier, instead of truly understanding anything about the other individual's perspective, the researchers conducted a control experiment. In the control condition there was also a physical barrier, but it was transparent. If the subordinate chimpanzees were just seeking physical protection, then this transparent barrier should have had the same effect as the opaque barrier, but it did not. When the barrier was transparent and the dominant chimpanzee could therefore see both food pieces, then the subordinate chimpanzees did not differentiate between the two locations (Hare et al. 2000).

In a later study Hare et al. (2006) showed that chimpanzees also actively conceal behavior from the view of a human competitor. As part of their decision which of two food pieces to approach, the chimpanzees had to decide which route to take based on the human's visual access to the two food pieces. While one approach route provided cover from the human's view, the other route did not. This was because, in a first condition, the human's face was oriented towards one piece of food but not the other, or, in a second condition, the chimpanzees could approach from behind either a transparent barrier or an opaque occluder. In a third condition, one piece of food was behind a barrier that fully shielded the chimpanzees' approach, while the other piece of food was behind a barrier that only partially shielded their approach. In all three conditions, the chimpanzees preferred to approach the food via the hidden route, which was not the case in situations during which no competitor was present (Hare et al. 2006).

Some researchers argue that, rather than understanding which route the human had visual access to, the chimpanzees in this study were following the more egocentric approach of simply avoiding the route from which they could see the human. Melis et al. (2006) tested this hypothesis by conducting another study in which chimpanzees competed with a human over two pieces of food. This time, both pieces were visible to the human but at no moment could the chimpanzees see the human while approaching one or the other piece. However, as there was a transparent tunnel leading to one piece of food and an opaque tunnel leading to the other piece, the human could observe the chimpanzee's hand reaching for one piece but not the other. In this situation (but not when they were alone and no competitor was around) chimpanzees preferred to reach through the opaque tunnel, presumably because they were able to imagine what the human could see from her – the human – perspective and understood that the human could not see their – the chimpanzee's – hand (Hare et al. 2006; Melis et al. 2006).

Interestingly, orangutans in a similar paradigm behave differently from chimpanzees. The orangutans in one study also preferred to reach through the opaque tunnel, but did so after initially inspecting (looking through) the transparent tunnel. This suggests that the orangutans' decision in this paradigm was driven more by egocentric behavioral preferences, such as avoiding the tunnel through which they could see the human (Gretscher et al. 2012).

That there might be significant species differences among the great apes when it comes to perspective-taking abilities is also supported by a study from Okamoto-Barth et al. (2007). In this study a human gazed in the direction of a target on the opposite side of a wall. In some situations a barrier was completely obstructing the human's view, whereas in other situations the obstruction had a window and the human could see the target. Chimpanzees, bonobos, and gorillas followed the human's gaze significantly more often when the obstruction had a window in it than when it did not – presumably because they understood that the human was actually able to see what was behind the barrier in one but not the other condition. The orangutans, however, did not differentiate between the two situations, suggesting that they did not attend to the human's perspective in this experiment (Okamoto-Barth et al. 2007).

Though there is convincing evidence that chimpanzees understand others' *visual* perspective, there is mixed evidence about chimpanzees' understanding of others' *auditory* perspective (Bräuer et al. 2007; Melis et al. 2006). While one study suggests that chimpanzees understand what other can and cannot hear (Melis et al. 2006), another study suggests that they do not (Bräuer et al. 2007). Melis et al. (2006) put chimpanzees in a competitive situation with a human over food. To get at the food the chimpanzees had to make the decision whether to reach through a noisy tunnel, which produced a loud rattling sound when opened, or through a silent tunnel. When competing with the human, the chimpanzees preferably reached through the silent tunnel, in an attempt to conceal their behavior. When the chimpanzees were alone and there was no competition, they did not differentiate between the two tunnels (see Santos et al. 2006, for similar results with rhesus monkeys).

Bräuer et al. (2007) put two chimpanzees, one dominant over the other, in a competitive situation over food and placed two obstacles between them. A human then placed one piece of food in a very noisy manner behind one of the obstacles. The subordinate saw that piece of food, whereas the dominant individual could only hear the placement. A second piece was then placed silently behind the second obstacle; again, the subordinate could see this take place, but the dominant had no information about the second piece of food. In this situation, subordinate chimpanzees did not prefer one piece over the other, indicating that they did not take the auditory perspective of the dominant individual into account. One significant difference between Bräuer's study and that of Melis et al. described above is that in the latter, the chimpanzees themselves produced the noise they heard, by reaching through the noisy tunnel; whereas in the study by Bräuer et al. the noise was produced by the human. A possible conclusion might be that it is easier for chimpanzees to attend to sound when they are the producer of the noise rather than just the noise receptor. It could also be, however, that the chimpanzees in Bräuer et al.'s study had simply learned that producing sounds in the experimental situation had consequences (Bräuer et al. 2007).

Primates' Understanding of Knowledge and Ignorance in Others

The evidence presented above shows that a number of different primate species can follow others' gaze, attend to others' attention, and, in some cases, have a flexible understanding of others' visual perspective. But going further, some primate species also seem to understand what others "know" – in the sense of having seen or experienced it in the past.

Hare et al. (2001) presented two chimpanzees, one dominant over the other, with a competitive situation over a piece of food. Between the two individuals were two opaque barriers. A human placed a piece of food behind one of the two barriers; either both chimpanzees watched this event or only the subordinate chimpanzee did. In the condition during which the subordinate knew that the dominant had not seen the food being placed, she reached for the food significantly more often than in the condition where the dominant had seen the placement. Subordinate chimpanzees also reached for the food in conditions during which the dominant had seen the initial placement of the food, but the food had then been moved to another location without the dominant's knowledge. They did so more often than in conditions during which the food was also moved to a new location but in full view of the dominant (Hare et al. 2001).

Kaminski et al. (2008) confronted chimpanzees with a situation during which two of the animals – one the actual experimental subject, and one serving as competitor – sat at opposite sides of a table. Mounted on the table was a sliding board with three cups on it, which a human slid back and forth between the two chimpanzees. Two of the three cups were baited with a piece of food. While the subject animal had witnessed the baiting of both cups and also had information on which cup remained empty, the competitor was only informed about one baited location, but had not witnessed the baiting of the second cup and also had no information as to which cup remained empty. In one condition, the competitor was the first to be given a choice between cups (and the subject did not see him do so), after which it was the subject's turn. If subjects understood that their competitor's choice was based on what the competitor had witnessed, they should then also understand that the one piece of food the competitor had seen being placed was now gone, and should aim for the other piece. This is exactly what the chimpanzees did. In this condition, the subject chimpanzees significantly preferred to pick the cup which contained the piece of food only they themselves had seen being placed. This was compared to a second condition, during which the general course of events was similar, except that this time, after the baiting was finished, it was the subject who got to choose first (and the competitor did not see that). Now subjects had the chance to maximize their food outcome if they changed their strategy and switched to a preference for the one piece of food the competitor had seen. When it was her turn, the competitor would then aim for an empty cup, which would give the subject the chance to obtain the second piece when it was her turn again. In this condition, chimpanzees did not show a preference for one over the other piece but chose randomly, indicating that they were not thinking prospectively (Kaminski et al. 2008). However, there was a significant difference between the two conditions in how often subjects aimed for the piece of food the competitor had not seen, indicating that the chimpanzees did not follow a simply associative rule like, e.g., "Avoid the piece of food the competitor has looked at."

That chimpanzees may even make inferences about other individuals' inferences is suggested by a study conducted by Schmelz et al. (2011), using a very similar paradigm to the one described above. Instead of cups there were two opaque boards on the table, and there was one piece of food hidden under one of these, resulting in that board being slanted. When their competitor had chosen before them, chimpanzees avoided the slanted board – presumably on the assumption that their competitor had already made the inference as to where the food was, based on seeing one board being slanted (Schmelz et al. 2011).

Taken together, the experimental evidence presented above suggests that chimpanzees have some understanding of knowledge and ignorance in others. This is also supported by evidence from wild-living chimpanzees. Crockford et al. (2012) showed that wild-living chimpanzees were more likely to produce alarm calls about a snake in the presence of group members who were not aware of the snake than in the presence of group members who were aware of it. This shows that chimpanzees monitor the knowledge states of their group members and can take them into account where appropriate (Crockford et al. 2011).

Primates' Understanding of Others' Intentions

In their original study, concerned with the question whether chimpanzees have a ToM, Premack and Woodruff (1978) designed an experiment to see whether Sarah, a female chimpanzee, was able to solve problems based on her understanding of others' intentions and goals. Understanding others' intentions is a highly beneficial skill for any species living in a complex social environment, as it enables the individual to anticipate others' behavior in certain situations. Sarah was shown videotaped scenes of a human actor being confronted with a variety of problems, e.g., an inaccessible banana or being locked in a compartment. Then Sarah was shown a series of photographs, one of which indicated the solution to the problem, e.g., a picture of a stick with which to reach for the inaccessible banana. Sarah had no difficulty picking the photograph depicting the solution to each respective problem. Premack and Woodruff (1978) argued that this could be seen as evidence that Sarah understood the human's goals and chose the correct means to the end. These studies were criticized, however, based on the suggestion that the problems posed could be solved by simple association and did not necessarily require for the chimpanzee to understand the human's goals (Savage-Rumbaugh et al. 1978).

Later Call and Tomasello (1998) confronted chimpanzees and orangutans with a situation during which a human indicated a baited box by placing a marker on top of it. The apes had no information about the location of the food and therefore relied on this communicative cue to find the correct location. Then the human placed a marker on top of each of two boxes. One marker was placed deliberately and intentionally, while the other marker, which ended up on the other box, was not placed with a clear intent but dropped seemingly accidentally. The apes clearly distinguished the boxes based on the human behaving differently towards each box, and on the level of intentionality with which the markers were placed. Again, one criticism of this study, as of that of Premack and Woodruff (1978), was that the chimpanzees required some training to understand that the marker indicated food, etc. The chimpanzees' behavior could therefore again be explained by association rather than by an understanding of others' goals (Call and Tomasello 1998).

Call et al. (2004) consequently designed a study in which no training was necessary. In this study the researchers compared chimpanzees' behavior in situations during which the human was either unwilling or unable to hand over a piece of food. The chimpanzees in this experiment were used to receiving their food through holes in a clear Plexiglas panel. When the human was unwilling to hand over the food, he would, e.g., merely present the food on his side of the glass, alternating his gaze between the food and the chimpanzee, but then pull the food back with no intention to hand it over. When the human was unable to hand over the food he would, e.g., present it while trying to pass it through a small hole in the Plexiglas panel – a hole through which it simply could not fit – and, while doing so, alternate his gaze between the food and the chimpanzee, then pull the food back after his failure to hand it over. The chimpanzees stayed away from the Plexiglas panel longer when the human was unwilling to give them food than when he was unable, indicating that they do distinguish these situations – presumably because they attend to the human's different goals in the different situations (Call et al. 2004; see Phillips et al. 2009, for similar results with capuchin monkeys).

Another context during which attending to others' goals is important is the social learning context. To copy another individual's actions successfully and focus on the relevant aspects of their behavior, it is beneficial for the observer to understand the demonstrator's goals. Gergely et al. (2002) did a study which suggests that human children imitate rationally, meaning that children in certain situations only copy another individual's actions when those actions represent intended behavior, but not when the behavior was produced because it was forced by certain constraints. The children in that study saw an adult switch on a light by pressing a button with his or her forehead. Sometimes use of the forehead was a choice, since the adult's hands were free, as visible for the child. At other times the adult was forced to use his or her forehead because the adult's hands were occupied. The children in this study copied the action of using the forehead to switch on the light more when it was the demonstrator's chosen action, but less when the action was forced because the person's hands were occupied. Buttelmann et al. (2007) designed a similar study for chimpanzees and confronted specially trained circus chimpanzees with a situation during which a human demonstrator performed a certain action. For example, very similar to the study by Gergely et al. (2002), the human would switch on a light with his forehead either with his hands free (which meant it was his choice to use his forehead) or with his hands occupied (which meant he was forced to use the forehead). These specially trained chimpanzees attended to the rationality of the human's actions, insofar as they copied those actions more often when they were freely chosen and less often when they were forced by circumstances (Buttelmann et al. 2007).

To see if great apes can infer others' goals based on contextual cues alone, without additional behavioral cues, Buttelmann et al. (2012) confronted apes with another situation during which food was handed over to them by a human. In order to hand over the food, the human at some point had to get up and step over a barrier, to reach one of two buckets from which he was feeding the apes. To see whether or not the apes simply anticipated what the human would do based on the latter's "intention movement" of getting up and stepping over the barrier, in the relevant experimental conditions there was additional contextual information which, if the apes could interpret it, would help to clarify the human's goals at the moment when the human was getting up. In one condition, for example, the human got a call through a walkie-talkie, which was placed on the floor. In this context the human's stepping over the barrier was necessary merely to pick up the walkie-talkie and talk to the other person. This was compared to a baseline condition during which the human stood up with the intent to feed the apes from the bucket and no additional contextual information was presented. The animals in this study clearly differentiated between these situations, presenting further evidence that apes not only attend and react to behavioral cues but might indeed interpret the human's goals in the different situations (Buttelmann et al. 2012).

Primates' Understanding That Others Have False Beliefs

As noted in the Introduction, the benchmark for the capability to attribute mental states to others is false belief understanding. This is because understanding that others have false beliefs requires a fully representational ToM (Wellman et al. 2001); it requires for the individual to understand that others' knowledge about the world can deviate from one's own, as well as from reality. As of yet, there is no evidence that any nonhuman animal can pass a false belief test.

Call and Tomasello (1999) designed a nonverbal false belief task for children as well as chimpanzees and orangutans. In this task one person (the "hider") hid a reward in one of two containers, and the other person (the "communicator"), after observing the initial hiding event, communicated the location of the reward to the subject by placing a marker on top of the baited container. The initial phase of the study showed that the children as well as the apes clearly understood the marker to be an indicator for the reward. In the actual false belief condition, the communicator had seen the baiting process but then left the area, upon which the other person, the hider, would switch the locations of the containers. Now the communicator's marking of one of the containers was wrong, since this person had a false belief about the location of the reward. Therefore, for subjects to get at the reward they now needed to avoid the location marked by the communicator, as reality contradicted the communicator's belief. The children in this setting had no problem solving the task and made the correct decision of avoiding the cup the communicator had marked in the false belief condition. The apes, however, still preferred the marked location, even if the marker in this situation was placed by a person who had a false belief about the container's content (Call and Tomasello 1999).

One problem with this study is that it is possible that the apes simply learned an associative rule – associating the marker with the food and never truly understanding it as a means to communicate. Another weakness is that the general structure of the paradigm is cooperative, when other studies have shown that chimpanzees seem to be most attentive to the general course of events when the context is competitive (Hare et al. 2001). Kaminski et al. (2008) therefore designed a study involving a competitive scenario. Two chimpanzees had to compete over a piece of desirable food. The animals sat opposite each other, with a table between them with three cups on it. Both chimpanzees, subject and competitor, had access to the three cups on the table and could choose alternately. The subject, however, had exclusive access to an additional cup, which also contained a piece of food – one which was of lesser quality than the piece of food on the table. This second piece of food served as the "opt out" option, which subjects could choose should they assume that all cups on the table are empty.

Both individuals then observed how the human placed the piece of high-quality food in one of the three cups on the table. After this initial baiting event, the human did one of two things: he either turned the cup and lifted the piece of food out again, then placed it back ("lift"); or, he turned the cup, lifted the piece of food, and then shifted it to another location ("shift"). The competitor either watched this second manipulation or not. The actual false belief condition was, therefore, the condition during which the food was shifted to a new location and the competitor did not see this. After all baiting was completed, the competitor always chose first; the subject did not see her choice. When it was the subject's choice, she had to make the decision whether to aim for the high-quality food on the table or, in case she assumed that it was gone, opt out and aim for the lower-quality food next to her. The chimpanzees in this situation aimed for the high-quality food significantly less often when the competitor had seen the second baiting event than when the competitor had not, which again supports the notion that chimpanzees are sensitive to knowledge ignorance in others. However, whether or not the food was only lifted (and the competitor's belief about its location was therefore still true) or shifted (and the competitor's belief about the location of the food was therefore false) did not affect subjects' choices, which supports the assumption that chimpanzees do not understand when others' beliefs are false (Kaminski et al. 2008).

This view is also supported by evidence from a study by Krachun et al. (2009), who set up a situation during which the chimpanzees competed with a human over food. The human competitor observed another, second person hide a reward in one of two containers. Then the competitor left the room (or turned around), and the other person switched the locations of the containers. The competitor re-entered and reached towards the container which he thought contained the food. While children tested in the exact same paradigm inferred that the competitor now had a false belief and therefore chose the container the competitor did *not* reach for, the apes did not attend to the competitor's false belief and did not avoid the container he reached for (Krachun et al. 2009).

Subsequently, in a looking paradigm designed by Marticorena et al. (2011) the authors showed that rhesus macaques, just like chimpanzees, understand knowledge ignorance in others but not false beliefs. In this study the monkeys, interacting with a human, looked longer at a location where they expected the human to search for an object the human had knowledge about. However, whether or not the human's belief about the location was false did not affect the monkey's looking behavior (Marticorena et al. 2011).

Conclusion

The ability to attribute mental states to others is a distinctive feature of human social cognition. Whether this is a uniquely human skill or shared with other species is highly debated. Recent research suggests that some primate species, especially the great apes, seem to understand certain psychological states in other individuals. It appears that primate species follow other individuals' gaze and consider it a relevant cue. Various primates, including monkeys and apes, are also sensitive to others' attention states. This is apparent in communicative situations during which primates modulate their gestural signals to the attentional state of the recipient. This ability seems to be rather widespread in the primate world, suggesting that it serves an important evolutionary function for gregarious species. There is also evidence in some primate species for the ability to take the visual perspective of others, and for an understanding that it can differ from one's own. While chimpanzees, humans' closest living relatives, also seem to understand something about others' knowledge and attention states, there is no evidence as yet that members of any primate species besides humans can understand when others' beliefs contradict reality and are therefore false. As false belief understanding is seen as the hallmark of a fully developed Theory of Mind, we need to take this as evidence that no nonhuman primate species have the capacity to truly attribute mental states to others.

Cross-References

- ▶ Cooperation, Coalition, Alliances
- ▶ Evolution of the Primate Brain
- ▶ Great Ape Social Systems
- ▶ Modeling the Past: The Primatological Approach
- ▶ Primate Intelligence
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ The Evolution of Speech and Language
- ▶ The Evolution of the Hominid Brain
- ▶ The Hunting Behavior and Carnivory of Wild Chimpanzees

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Part III

Phylogeny of Hominins

Potential Hominoid Ancestors for Hominidae

George D. Koufos

Contents

Abstract

Human origin and evolution are a prominent topic among scientists, one on which there continues to be disagreement. Each new finding raises new questions and arguments. This chapter summarizes the currently available data and hypotheses on hominid origins. The origin of the hominids may be traceable to Oligocene anthropoids such as *Aegyptopithecus*, which share some derived features with the early hominoids. The Latest Oligocene taxon *Kamoyapithecus* could be the oldest known hominoid, as it has relationships with some Miocene taxa. *Proconsul* is the most plausible taxon linking the hominoids to the great ape and human clades, as it preserves a mosaic of features from both groups. The Middle Miocene European hominoids seem to play an important role, and could include the possible link between more archaic hominoids and the great ape and human clades; candidates are numerous among both European and African forms. Among Late Miocene taxa, the craniodental morphology of

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G.D. Koufos (✉)
Laboratory of Geology and Palaeontology, Department of Geology, Aristotle University of Thessaloniki, Thessaloniki, Greece
e-mail: koufos@geo.auth.gr

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Ouranopithecus provides the closest and most plausible link connecting the hominoids to the extant great apes and humans; its strong relationships to the australopiths and *Homo* put this taxon among the best candidates for this role at the moment. The Latest Miocene *Sahelanthropus* and *Orrorin* seem to be important links in the evolution of the hominids, whereas the Asian Middle-Late Miocene hominoids have strong similarities with the modern orangutans and are related to the "*Pongo*-lineage."

Introduction

The presence, origin, and future of man on earth are problems that have long preoccupied humans. Questions like "Who is my ancestor?", "What was it like?", or "Where do I come from?" were among the first for which answers were sought. Humanity's need to find answers to these questions led, first, to origin myths, and later, after the development of science, to theories of human origins. Anthropology and biology offer answers based on the comparative anatomy, behavior, and genetics of humans and other animals. The evolutionary approach to understanding human origins seeks to identify all the characters that humans share with apes (our closest relatives) and with other animals. The ancient Greek philosopher Aristotle was among the first to recognize the affinities of man with the animals and placed man in the animal kingdom. Much later, the Swedish taxonomist Linnaeus classified humans laterally to the apes and monkeys, while the pre-Darwinian French naturalist Buffon as well laid out the view that humans have similarities with the apes, creating a link in the long chain of the beings.

Paleoanthropology is the branch of paleontology that addresses the above questions based on the primate fossil record. Paleoanthropologists try to find the links between various fossil and extant taxa in order to complete the "chain" leading to humans. This is difficult and time-consuming work, as fossils are relatively rare and widely dispersed; in most cases the remains are fragmentary, providing limited data. The discovery of new fossils over the last 50 years and the development of new methods for studying, comparing, and dating fossils, as well as for reconstructing their locomotion and paleoenvironment, have significantly increased our knowledge about the morphology and evolutionary relationships of primates. One of the main goals of paleoanthropology is to find the ancestor of humans – usually referred to as "hominids" – among the common stock of hominids and apes – known as "hominoids". The hominoids constitute a group of African and Eurasian forms that lived during the Miocene epoch and are assumed to include the common ancestor of humans and apes.

The following is a brief sketch of what we know about the hominoids. Later sections of this chapter will go into more detail on evidence from different time periods. The chapter does not answer what are still open research questions; its goal is merely to survey the available data about the potential hominoid ancestor of the hominids, providing a comprehensive overview.

The first known hominoids are from Africa. The earliest possible representative of the hominoids originates in the Oligocene, the time of the genera

Aegyptopithecus and *Kamoyapithecus*. Hominoids are more securely represented by the large set of Early Miocene proconsulids. The majority of the Early Miocene hominoids are restricted to Africa and are only found in East Africa and the Arabian Peninsula. A large number of taxa are recognized (*Proconsul, Afropithecus, Heliopithecus, Nyanzapithecus, Mabokopithecus, Rangwapithecus, Turkanipithecus, Dendropithecus, Micropithecus, Simiolus, Morotopithecus, Limnopithecus, Kalepithecus*), but most of them are known from only a few fragmentary fossils. Their size varied from small monkey sized (~3 kg) to large great ape sized (~80 kg), while their locomotion was quadrupedal and arboreal. The majority were fruit or leaf eaters. *Kenyapithecus*, who appeared at the end of the Middle Miocene (~14 Ma), was probably a hard-object feeder. The uppermost Middle Miocene and Late Miocene hominoids of Africa are rare and poorly known compared to Early/Middle Miocene forms (*Kenyapithecus, Samburupithecus, Otavipithecus, Orrorin, Equatorius, Sahelanthropus*).

Towards the end of the Middle Miocene, the "story" of hominoid evolution continued in Eurasia, where hominoids were abundant until the Late Miocene (~7.5 Ma). Hominoids that migrated to Eurasia are represented by the taxa *Griphopithecus* and *Kenyapithecus*. After their arrival, they strongly diversified; several new taxa (*Dryopithecus, Pierolapithecus, Anoiapithecus, Oreopithecus, Ouranopithecus, Sivapithecus, Ankarapithecus, Lufengpithecus*) appeared between 8.0 and 13.0 Ma. The size of these taxa varies from medium to large, while their dietary type ranges from soft-object feeders, like *Dryopithecus* and *Oreopithecus*, to hard-object feeders like *Ouranopithecus, Ankarapithecus, Lufengpithecus*, and *Gigantopithecus*. Postcranial remains are relatively rare, and the available material indicates quadrupedal locomotion; however, one of these taxa, *Pierolapithecus*, is interpreted as an early orthograde (Moyà-Solà and Köhler 1996).

The occurrence of the oldest australopithecines is dated to ~4.5 Ma, whereas the last Miocene hominoids date to the Middle Turolian (~7.5 Ma). There is thus a large gap of ~3 Ma between them. Until the beginning of the twenty-first century, no fossils were known from this time interval. The discovery in 2000 of the African hominoid *Orrorin*, dated to ~6 Ma (Senut et al. 2001), provided the first evidence to fill the gap. One year later, the skull of *Sahelanthropus*, found in Chad and dated to 6.0–7.0 Ma, offered more data about this unknown time interval (Brunet et al. 2002). Most recently, some cranial remains of a hominoid from the Turolian of Turkey (Begun et al. 2003; Güleç et al. 2007) and an isolated tooth of a hominoid possibly from the Middle Turolian of Bulgaria (Spassov et al. 2012) have added further evidence.

Origin of the Miocene Hominoids

The origin of the Miocene hominoids is to be found among the Oligocene primates. The division of the anthropoids into two main groups – the Platyrrhini (New World monkeys) and the Catarrhini (Old World monkeys) – is thought to have occurred at the Eocene/Oligocene boundary. One of the oldest and best-known catarrhines is

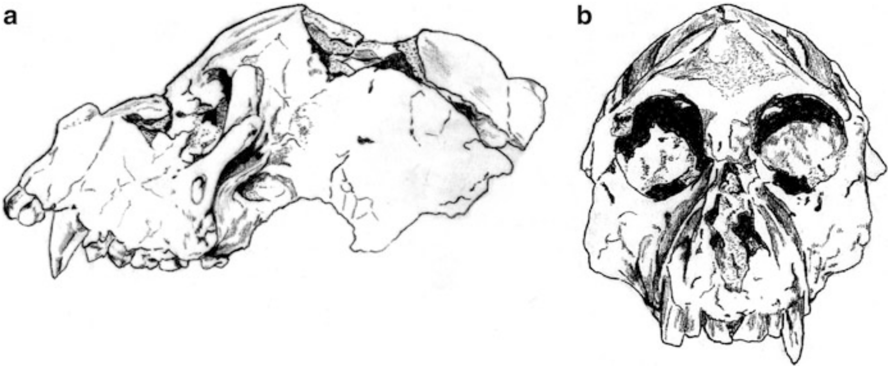

Fig. 1 *Aegyptopithecus zeuxis*, sketch of the skull found in 1966. (**a**) Lateral and (**b**) frontal view (Drawn from the photo of Szalay and Delson (1979; Fig. 222))

Aegyptopithecus (Fig. 1), from the Fayum province of Egypt, with an estimated age from 32.0 to 35.0 Ma (Tattersall et al. 1988). Since the Eocene/Oligocene boundary is estimated to be at ~35 Ma, the splitting of the catarrhines and platyrrhines coincides with the beginning of the Oligocene and bridges the gap between the Eocene Prosimii and the Miocene hominoids.

Aegyptopithecus preserves some characters of the platyrrhines, such as the absence of an auditory tube in the external ear, but it has two premolars in each half of the jaw, a feature that serves to classify it within the catarrhines, being among the most primitive of them. The main morphological characters of *Aegyptopithecus* (Fig. 1) are an elongated skull with strong prognathism, strong postorbital constriction, large and completely enclosed orbits, weak supraorbital torus, large interorbital distance, a posteriorly developed sagittal crest, well-developed sexual dimorphism in the canines, and broad molars with rounded and low cusps, well-developed cingulum, and thin enamel. The braincase is small: its capacity is estimated at ~30 cm^3 (Conroy 1990). The endocasts indicate morphology falling between the primitive and more derived anthropoids (Radinsky 1973). The humerus is relatively stout, with a large medial epicondyle and relatively wide trochlea. The morphology of the metapodials and phalanges suggests powerful grasping. The overall morphology of *Aegyptopithecus* indicates quadrupedal climbing, while the morphology of the skull and teeth suggests a soft-object feeder. This type of diet fits well with its postcranial morphology, indicating a good climber.

The presence of some derived characters in *Aegyptopithecus* has been interpreted in different ways. Simons (1965), focusing on features shared between *Aegyptopithecus* and *Proconsul*, suggested a close phyletic relationship between the two genera. Later, Andrews (1978) reported close similarities between the upper molars of *Aegyptopithecus zeuxis* and *Proconsul africanus*, but could not identify clearly shared derived features. The cranial proportions and the external ear showing a clear auditory tube in *P. africanus* are more derived features than those of *Aegyptopithecus* (Szalay and Delson 1979). The primitive robust postcrania of *Aegyptopithecus*, with less joint mobility, suggest relatively more leaping locomotion, whereas in the Miocene hominoids leaping constitutes only a small share of locomotion (Gebo 1993). Tattersall et al. (1988) suggested that *Aegyptopithecus* represents an early catarrhine close to the split between platyrrhines and catarrhines. *Aegyptopithecus* is a mosaic of primitive and derived characters, linking Eocene anthropoids to modern apes and monkeys, and could represent or be close to their common ancestor – a notion evidenced by its Greek species name *zeuxis*, meaning "way of connecting, bridge." However, the available data do not fully support this view. Despite the possible link between *Aegyptopithecus* and the hominoids, there is no clear bridge, but in fact a 10.0 Ma gap in the fossil record between *Aegyptopithecus* and the first Miocene hominoids.

The earliest possible representative of the hominoids is the Latest Oligocene *Kamoyapithecus* from Lothidok (Kenya), which is dated from 27.8 to 23.9 Ma (Leakey et al. 1995). The large size of *Kamoyapithecus*, although not decisive evidence, is similar to that of some early Late Miocene apes, suggesting that it could be the earliest known hominid (Leakey et al. 1995). During the Oligocene, several Afro-Arabian taxa of early catarrhines are known to have existed (*Catopithecus, Oligopithecus, Moeripithecus, Propliopithecus*), which could also be related to the Miocene hominoids.

The Miocene Hominoids

Whereas the Eocene was the period of the prosimians and the Oligocene that of the early anthropoids, the subsequent Miocene represents the epoch of the hominoids, with many named genera and species. The taxonomic expansion is due in part to the limited material evidence allowing for differences in opinion among scientists, and in part to a tendency among paleoanthropologists to postulate new taxa. The hominoids expanded across the Old World from Spain to China and from South Africa to northern Europe (Fig. 2). During the last 40 years, extensive field campaigns carried out in the Old World by several scientific groups have brought to light numerous fossils. In addition, the revision of old material and new "discoveries" made in museum collections have increased the Miocene hominoid fossil record. This great knowledge gain of the last decades has led to the recognition of several new taxa, well defined through the application of several new methods, and to the recognition that the Miocene was an epoch of high diversification among hominoids.

During the Miocene, several geotectonic movements took place in the Old World that caused geographic and environmental changes with either positive (diversification, expansion, migration) or negative (reduction or even extinction) effects on the hominoids. Many new hominoids appeared in Eurasia after their arrival from Africa during the upper part of the Middle Miocene. For a long time scientists believed that the Turolian dryness and the arrival of the cercopithecids were the main reasons for the extinction of the hominoids at the end of the Vallesian

Fig. 2 Geographic map indicating the most important sites with hominoids; *blue square* = Oligocene and *red circle* = Miocene localities

in Eurasia. This idea changed after the discovery of Turolian hominoids in Turkey and Bulgaria (Güleç et al 2007; Spassov et al. 2012). In Asia *Gigantopithecus* survived, as we know from finds in the Pleistocene of Southern China and Vietman (Kelley 2002). In Africa, hominoids existed in the Turolian as well; new discoveries during the last years have increased our estimate of their number (Kunimatsu et al. 2007; Brunet et al. 2002; Suwa et al. 2007; Senut et al. 2001). The paleogeographic and paleoclimatic changes that took place during the Miocene were strong factors contributing to the rapid evolution and diversification of the hominoids, leading to more derived and better adapted forms. Although the increasing severity of the ecological conditions eventually caused the extinction of most Miocene hominoids, for some of them the environmental pressure created an opportunity to develop comparatively more derived and evolved characters, which enabled their adaptation to the new conditions.

As mentioned above, *Aegyptopithecus* and *Kamoyapithecus* might be the ancestors of the Miocene hominoids; the possible common ancestor of humans and apes, then, must be looked for among the stem Miocene hominoids. From this point of view, the hominoids are a very important and interesting group of primates. Over the last 50 years, several hominoids have been presented as possible ancestors of the hominids, but so far there is no one candidate that has clearly won out. The problem is complicated and cannot be solved easily, as the relationships among the fossil hominoids, as well as between extinct and extant members of this superfamily, are not fully known. The data for the fossil hominoids in most cases are limited and do not permit clear definitions and comparisons. The number of specimens is another problem. No fossil hominoid is known well enough to allow for complete understanding of its morphology and relationships. There are several important time gaps between the various forms, which prevent clear establishment of their relationships. When there is so much uncertainty to contend with, subjectivity of interpretation is also an issue: it can be difficult for researchers not to engage in speculation. As we proceed below to discuss the evidence for the most probable ancestors of the hominids, the Miocene hominoids, these caveats must all be borne in mind.

Knowing the age of fossil hominoids is important for establishing their evolutionary relations. Yet here too lies a source of uncertainty and debate. Efforts at age determination must often confront contradictory data and give rise to differences of opinion. Nevertheless, for most hominoids satisfactory age correlation has been achieved by either biochronology, or radio-/magneto-chronology, or both. The stratigraphic distribution of the main Miocene hominoids of Africa and Eurasia is given in Fig. 3. The figure also shows the European land mammal stages and zones, which are mentioned in the text. The continuous line indicates the stratigraphic distribution of the taxa, the dashed line their possible distribution, and an asterisk denotes that the taxon is known from a single site or all known material has similar age. It is quite clear from Fig. 3 that the hominoids are already well known from the Early–Middle Miocene of Africa, while in Eurasia, they are more common during the Late Miocene.

The Early Miocene

Early Miocene hominoids are known only from Africa. The best known taxon is *Proconsul* (Fig. 4) (Walker 1997). The oldest remains of *Proconsul* (*P. africanus, P. major*) were found in Kenya and Uganda and are dated to 19.0–20.0 Ma. Two other species (*P. nyanzae* and *P. heseloni*) are known from Kenya and dated to 17.0–18.5 Ma (Harrison 2002) (Fig. 4).

Proconsul has an estimated body size that varies from that of a small monkey to that of a female gorilla. It shows sexual dimorphism in body size, as well as in the size and morphology of the canines. This sexual dimorphism is a primitive feature for *Proconsul*. The nasomaxillary region of *Proconsul* has a primitive internal structure with a large fossa incisiva. In addition, the maxillary processus palatinus is clearly lower than the premaxilla (Ward and Kimbel 1983; Ward and Pilbeam 1983). This nasomaxillary morphology ("African type," according to the latter authors) is similar to that of *Australopithecus, Dryopithecus, Ouranopithecus*, and the recent *Gorilla*. The skull has a moderately short and broad face compared to that of *Aegyptopithecus*, and a broad and relatively rhomboid-shaped nasal aperture, trapezoid orbits with rounded corners, a slight supraorbital torus with slightly swollen glabella, and a clear auditory tube like the recent cercopithecoids and hominoids (Szalay and Delson 1979; Walker 1997; Harrison 2002).

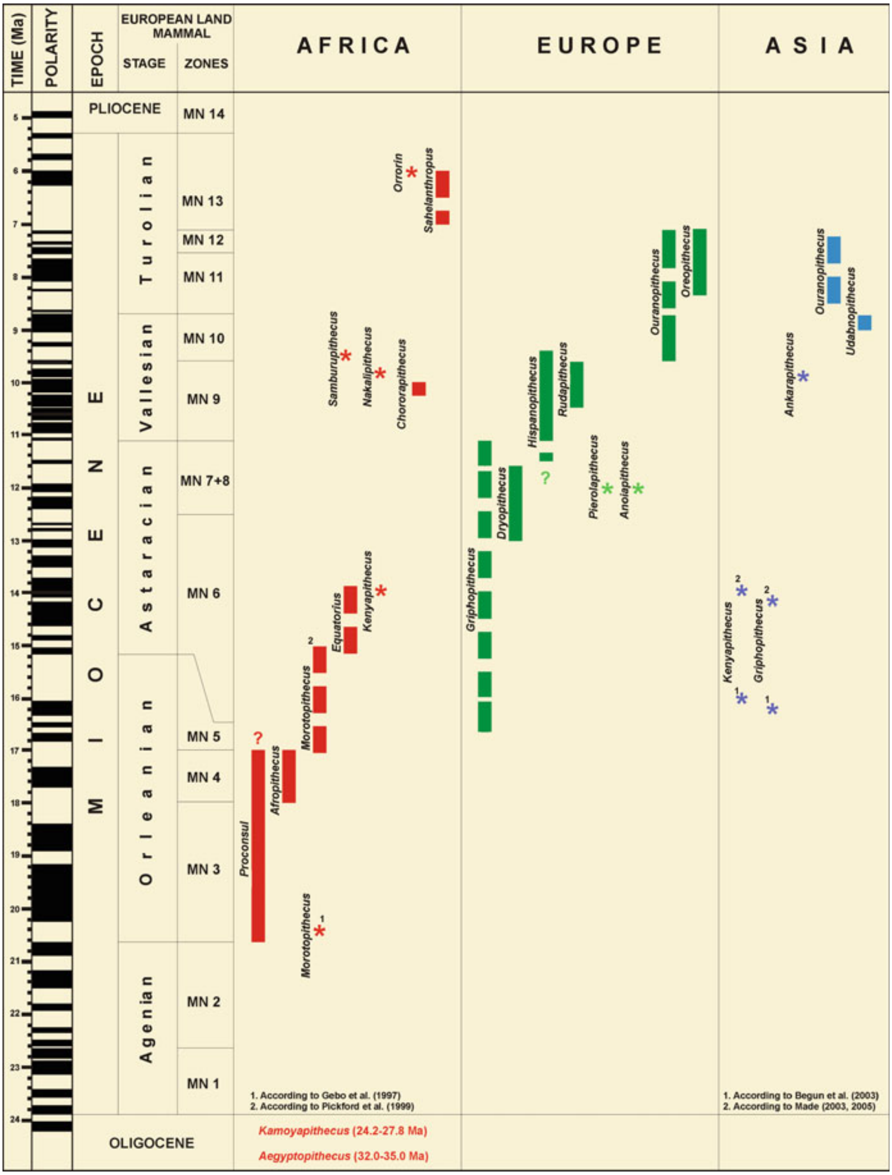

Fig. 3 Stratigraphic distribution of the main Miocene hominoids; *continuous line*: stratigraphic distribution of a taxon; *dashed line*: possible distribution of a taxon; *asterisk*: taxon known from a single site or from several localities of the same age

The dentition of *Proconsul* preserves primitive features, such as relatively long and broad canines, a well-developed cingulum, asymmetric upper premolars with large paracones (buccal cusps), and the presence of a honing facet on the P3. Although the dental morphology of *Proconsul*, which indicates a soft fruit feeder

Fig. 4 *Proconsul heseloni*. Sketch of the first skull found in 1948 by M. Leakey on Rusinga Island, Lake Victoria (Drawn from a photo of Harrison (2002))

(Kay and Ungar 1997), is well known, there are no clear synapomorphies with either the hominoids or the cercopithecoids. In many ways, it is similar to the dentition of the Oligocene Fayum catarrhines.

The known postcrania of *Proconsul* are relatively abundant and provide a large set of characters. However, the systematic interpretation of these characters leads to contradictory results. *Proconsul* has anterior and posterior limbs of more or less similar length, indicating quadrupedal arboreal locomotion. The recent hominoids have a more erect posture (knuckle walking and brachiation). The robustness of the long bones of *Proconsul* suggests similarities to cercopithecoids, chimpanzees, and to ceboids with less elongated limbs. The distal extremity of the *Proconsul* humerus resembles that of small apes, while the distal extremity of the ulna is relatively straight, as in most anthropoids. The carpals indicate a climbing primate, whereas the phalangeal proportions are very close to macaques, suggesting a quadrupedal form (Walker and Pickford 1983; Ruff et al. 1989; Rose 1992, 1993).

Most authors consider *Proconsul* to be a stem hominoid close to the origin of the Hominoidea (Hopwood 1933; Pilbeam 1969; Rose 1983, 1992, 1993; Andrews 1985; Begun et al. 1997; Kelley 1997; Ward 1997). These authors conclude that *Proconsul* shared derived characters with the extant hominoids. A different opinion suggests that *Proconsul* is a sister taxon of the recent great apes and humans (Walker and Teaford 1989; Rae 1997; Walker 1997). Neither opinion is accepted by Harrison (2002), whose detailed and critical analysis of key synapomorphies of the face, ear region, and postcrania shared by extant hominoids leads him to conclude that these are lacking in *Proconsul*. In contrast, Walker (1997) does refer to shared derived characters between *Proconsul* and more advanced hominoids, but he also recognizes possible features in the postcrania indicating a primitive catarrhine.

The frontal sinus in the skull of *Proconsul* could be a derived character – one shared with the extant hominoids and great apes (Andrews 1992). Although the frontal sinus is absent in Old World monkeys, it is clearly present in New World monkeys, which complicates the analysis of this feature. The absence of a tail is a derived character of the hominoids; the lack of a tail in *Proconsul* (Ward et al. 1991) thus suggests a relationship to the hominoids. The presence of six lumbar vertebrae rather than seven in *Proconsul* (Ward et al. 1993) also indicates a similarity to the hominoids and distinguishes it from monkeys. Several characters of the phalanges could be derived and shared with extant apes (Begun et al. 1994). The morphology of the trapezium and first metacarpal of *Proconsul* could be viewed as derived, with several characters shared between *Proconsul* and extant hominoids (Rose 1992). The relatively greater deviation of the ulna of *Proconsul* is, again, a derived character of the hominoids (Beard et al. 1986); in non-hominoid catarrhines the deviation of the ulna is not as strong. Rae (1997) studied a set of facial characters in the Early Miocene and modern hominoids and found that Early Miocene hominoids, including *Proconsul*, are linked to modern hominoids, in particular to great apes. As mentioned, Walker (1997) recognized *Proconsul* as a morphologically primitive hominoid, sharing several derived characters with the extant hominoids.

In sum, *Proconsul* has a set of characters that link it with the Miocene hominoids, and even with the extant great apes and humans, but controversies remain. Future research may provide additional data, permitting more definitive conclusions about its phylogenetic relationships.

In addition to *Proconsul*, several other taxa are known from the Early Miocene of Africa that could be related to the extant great apes and humans. It is appropriate here to give some information about the most important of them and their relationships.

The genus *Afropithecus* was recognized in Kenya based on finds from localities dated to the early Miocene; the age of these finds is estimated between 17.0 and 18.0 Ma (Leakey and Walker 1997). *Afropithecus* is characterized by its relatively large size (similar to the recent chimpanzee), long and wide skull, narrow palate, large diastema, narrow and protruding premaxilla, large interorbital distance, asymmetrical orbits, slender supraorbital torus, frontal sinus extending to the glabella, lack of the superior transverse torus in the mandible, and an oblique angle between ascending ramus and mandibular corpus. The upper canine has a round basal section and deep mesial groove, while the lower canine is low crowned and laterally compressed. The upper premolars are wide and without lingual cingulum, while the cusps are moderately heteromorphic. The upper molars are narrow, with moderately developed lingual cingulum and very thick enamel. The dentition of *Afropithecus* thus differs clearly from that of *Proconsul* (Begun 2013), but the few known postcrania resemble those of *P. nyanzae* in size and morphology (Leakey and Leakey 1986; Leakey et al. 1988; Leakey and Walker 1997; Ward 2007).

Afropithecus is a large hominoid whose facial shape resembles that of *Aegyptopithecus zeuxis* (Leakey et al. 1991), but whose postcrania are more derived than those of *Aegyptopithecus* and closer to *Proconsul* (Harrison 2002; Ward 2007). The teeth of *Afropithecus* are more derived than those of the Oligocene forms, featuring enlarged and procumbent incisors and thick canines. These characters as well as the very thickly enameled teeth suggest a hard-object eater, which places *Afropithecus* closer to *Kenyapithecus*. The lack of these characters in the dentition of *Proconsul* indicates a less derived feature, but its derived facial shape is closer to the later hominoids.

Morotopithecus is known from Uganda from a single species, *M. bishopi*, which was originally described as *Proconsul major*. Its age is debatable: the correlation of the fauna and older K^{40}/Ar^{39} datings suggest a Middle Miocene age, 17.0–15.0 Ma (Bishop et al. 1969; Pickford et al. 1999), whereas $^{40}Ar/^{39}Ar$ datings suggest an Early Miocene age at ~20.6 Ma (Gebo et al. 1997). *Morotopithecus* is relatively small sized, smaller than *P. major*. The skull is characterized by a long, high, and narrow face, short premaxilla, wide palate, narrow interorbital distance, large diastema, and a primitive nasomaxillary region with a large fossa incisiva. There is strong sexual dimorphism in the upper canines. The upper premolars are broad and relatively large. The molars have bunodont cusps, wrinkled enamel, and a well-developed lingual cingulum, similar to those of *P. major* (Pilbeam 1969; Andrews 1978; Harrison 2002). Although *Morotopithecus* differs from *Proconsul* in several features, its cranial and dental characters suggest that it is closer to the proconsulids.

The postcrania of *Morotopithecus* are few but provide some significant characters for the genus. The anatomy of the lumbar vertebrae shares some derived features (robust pedicles, reduced ventral keeling) with the extant hominoids. The scapula (some authors do not agree that it belongs to this genus) has a rounded and expanded upward glenoid articular surface, as in hominoids. Finally, the morphology of the femur and phalanges resembles that of *Proconsul* and indicates an arboreal form (Walker and Rose 1968; Gebo et al. 1997; MacLatchy et al. 2000; Harrison 2002). On the basis of its postcranial morphology, *Morotopithecus* could be considered as belonging to the Hominoidea (Gebo et al. 1997; Harrison 2002). However, Andrews (1992) reported that the morphology of the skull and teeth of *Morotopithecus* are less derived than in proconsulids, while the upper teeth share derived features with afropithecines. Thus *Morotopithecus* seems to belong to the Hominoidea given its postcranial morphology, but to pattern with the proconsulids in its cranial and dental characters. It is recognized as a stem hominoid (Gebo et al. 1997; MacLatchy et al. 2000; Harrison 2002). Harrison (2002) raises the question whether the derived features of the vertebral column might be an adaptation to increased orthogrady.

As apparent from this overview, a great number of Early Miocene hominoid taxa are included in the proconsulids, but the majority is known from only one specimen or isolated teeth. They are referred to under various names, and as mentioned, their relationships to each other, as well as to the other extinct and extant hominoids, are questionable. Nevertheless, the ancestor of the Early/Middle Miocene hominoids is now deemed to be a member of this group. The reason is that taxa like *Proconsul* seem to have more similarities to the later hominoids in their various derived characters, while also retaining some primitive features. The derived characters of the face, the teeth, and the postcrania of the proconsulids allow for any one of them to have a close relationship to the younger forms.

The Middle Miocene

Compared to the Early Miocene African hominoids, the Middle Miocene ones are few in number. One of the most important taxa is *Kenyapithecus*, known from Kenya (Leakey 1962) and dated to 14.0 Ma (Kelley and Pilbeam 1986). It is a medium-sized hominoid with clear canine fossa, highly zygomatic arches, clear sexual dimorphism, strong inferior torus, robust mandibular corpus, less asymmetric P4, large upper molars without lingual cingulum, and a P3 with a honing facet and buccal cingulum (Ward and Duren 2002). Few postcrania of *Kenyapithecus* are known, but those that have been found display some evolved characters, such as a posteriorly directed medial epicondyle and a wide trochlea in relation to the breadth of the capitulum of the humerus (Andrews and Walker 1976). The phylogenetic relationships of *Kenyapithecus* are still debated. *Kenyapithecus* has derived mandibular and dental characters (larger inferior than superior transverse torus, relatively short and wide corpus) that are shared with extant hominoids. Compared to the Early Miocene hominoids, it is characterized by a reduction or absence of cingulum in the molars, an increase of the enamel thickness, large upper premolars relative to the molars, and a more molarized dp3 close to that of *Gorilla* and *Pan* (McCrossin and Benefit 1997). All of these features are shared with *Ouranopithecus, Sivapithecus*, and *Griphopithecus*.

Equatorius is a Middle Miocene African hominoid found in Kenya. It is dated between 15.5 and 14.0 Ma (Feibel et al. 1989; Ward et al. 1999). *Equatorius* is medium sized, with strong sexual dimorphism, more symmetrical upper premolars, reduced or absent lingual cingulum, less heteromorphic lower premolars, thick enamel, as well as a P3 with a honing facet and variably developed buccal cingulum. It is considered a primitive hominoid, belonging to a derived clade of *Afropithecus* (Ward and Duren 2002).

The morphological characters of the teeth and mandible of *Equatorius* and *Kenyapithecus wickeri* suggest that there is no generic difference between the two taxa, which can be synonymized (Benefit and McCrossin 2000). Begun (2000) questioned the generic distinction between *Equatorius* and *Griphopithecus* from Europe, suggesting evidence of a biogeographic link between the two. Ward et al. (1999) and Kelley et al. (2000) reported that the incisor, canine, and maxillary morphology of *K. wickeri* are more derived than in *Equatorius* and distinguish the two genera. The robust mandible and the large inferior torus of *Griphopithecus alpani* (known from Paşalar and Çandir, Turkey) are similar to those of *Kenyapithecus*, but the upper jaw is less robust than that of *Equatorius*, while the dental morphology is similar (Andrews and Harrison 2005). Moreover, *K. wickeri* exhibits similarities to the rarely represented hominoid of the Paşalar sample, which are enough to attribute both to the same genus (Martin and Andrews 1993; Ward et al. 1999; Kelley et al. 2000) (see below).

The Eurasian Middle Miocene hominoid fossil record is richer than the African one and includes several genera. *Griphopithecus* was originally found in the locality of Devinska Nova Ves of Slovakia (Abel 1902), and was later recognized in the localities of Klein-Hadersdorf, Austria (Steininger 1967), and Engelswies, Germany, by the species *G. suessi* (Heizmann 1992; Heizmann et al. 1996), as well as in Paşalar and Çandir, Turkey, by the species *G. alpani* (Andrews et al. 1996). The fossiliferous site Engelswies is considered the oldest in Eurasia; it is designated to the European Mammal Zone MN 5 (Mein 1999). According to Casanovas-Vilar et al. (2011), the localities of Devinska Nova Ves and Klein-Hadersdorf might be younger than 11.6 Ma, corresponding to the upper part of the European Mammal Zone MN 7 + 8 or younger. A similar uncertainty surrounds the age of the Turkish localities; they are correlated either to the European Mammal Zone MN 5 (Begun et al. 2003) or to MN 6 (Made 2003; 2005), (Fig. 3). Considering these data, it seems that the history of the hominoids in Eurasia starts at ~16.0 Ma. According to Rögl (1999) the physical connection between Africa and Eurasia was gradually completed during this period. Three main migration waves are recognized to have occurred at that time, including the arrival of the hominoids in Eurasia.

Griphopithecus is comparable in dental size to *Pan*, and has a robust mandible, strong superior and inferior transverse torus, very elongated and strongly inclined planum alveolar, and low-crowned molars with rounded cusps, thick enamel, and a buccal cingulum. The few known fragmentary postcrania indicate an arboreal adaptation (Begun 2002; Kelley 2002). *Griphopithecus* fossils consist mainly of isolated teeth and are difficult to use as evidence for establishing phylogenetic relationships either to the African Middle Miocene hominoids or to the Late Miocene Eurasian ones. The limited maxillary and mandibular fragments from Paşalar preserve mainly primitive hominoid characters (Andrews et al. 1996). The taxon's relationships with the Late Miocene Eurasian hominoids are not clear.

A second, rare Paşalar hominoid was described as a new species under the name *Kenyapithecus kizili* by Kelley et al. (2008). It shares several characters with the African *K. wickeri*, such as the robust and moderately deep maxillary alveolar processes, the restricted maxillary sinus, and the zygomatic process which originates almost above the alveolar margin (Kelley et al. 2008). The presence of *Kenyapithecus* in Paşalar is a piece of evidence linking the African and Eurasian hominoids.

A rich sample of Middle Miocene hominoids has been recovered from the Vallès Penedès Basin (Spain). The material was discovered in the long section of Abocador de Can Mata. It is ascribed to three different hominoid taxa: *Pierolapithecus catalaunicus, Anoiapithecus brevirostris*, and *Dryopithecus fontani*, (Moyà-Solà et al. 2004, 2009a, b) (Fig. 5).

Pierolapithecus catalaunicus is known by a partial skeleton; it is dated to the European Mammal Zone MN 7 + 8, with an estimated age of ~11.9 Ma (Moyà-Solà et al. 2004). The main characters of *Pierolapithecus* are a low face, flat nasals, posteriorly situated glabella, highly originated zygomatic arches situated anteriorly

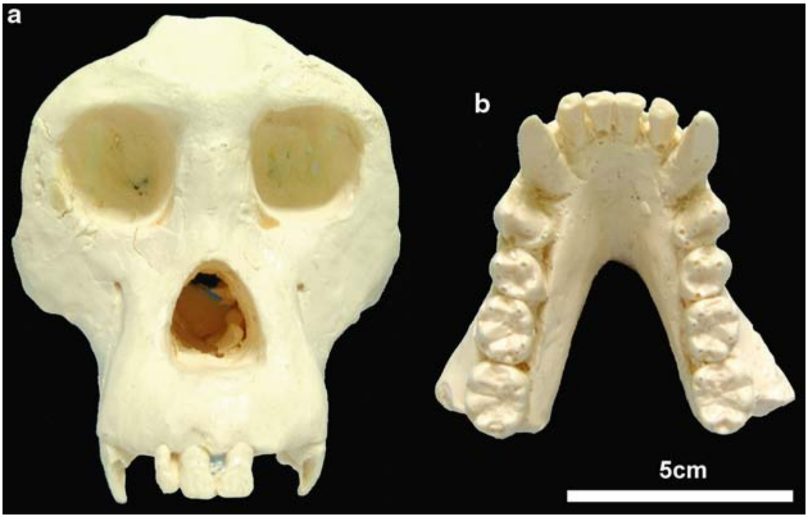

Fig. 5 (**a**) *Dryopithecus laietanus*, Can Llobateres I, Vallès Penedès, Spain. Cast of the reconstructed skull CLI 18000; (**b**) *Rudapithecus hungaricus*, Rudabànya, Hungary. Cast of the mandible RUD-14; the casts are to me by D. Begun

at the level of M1, high nasoalveolar clivus, reduced heteromorphy in the premolars, elongated molars, absence of a cingulum, large, low-crowned, and compressed upper canines, strong rib curvature, a large and robust clavicle, and short metacarpals and phalanges. The morphology of the thorax (wide and anteroposteriorly shallow), the lumbar vertebrae, and the wrists indicate suspensory, orthograde adaptations. The facial morphology displays the main derived characters of the extant great apes. *Pierolapithecus* retains some primitive characters, such as the short phalanges, suggesting palmigrade features. The overall facial and dental structures of *Pierolapithecus* indicate that it is probably close to the last common ancestor of great apes and humans (Moyà-Solà et al. 2004).

The second Spanish hominoid found in Abocador de can Mata, named *Anoiapithecus brevirostris*, is dated at ~11. 9 Ma (Moyà-Solà et al. 2009a). Despite its primitive features (low-crowned teeth, labial and lingual flare in the cheek teeth, short roots in the canines, heteromorphic cusps in the upper premolars) and the autapomorphic facial morphology, *Anoiapithecus* shares some characters with the afropithecids and the Middle-Late Miocene hominoids (Moyà-Solà et al. 2009a). According to last authors the combination of some autapomorphic features of this taxon with the kenyapithecines and hominid synapomorphies, as well as the presence of both groups in Eurasia during the Middle Miocene, support the “Back to Africa” hypothesis.

Among the Middle Miocene hominoids of Europe, *Dryopithecus fontani* is one of the oldest known from western and central Europe (Fig. 3). It was originally described from La Grive, France, and is correlated to the European Mammal Zone MN 7 + 8 (Casanovas-Vilar et al. 2011). According to Moyà-Solà et al. (2009b), the facial pattern of *D. fontani* resembles that of *Gorilla*; this resemblance could indicate an early member of the hominins or a stem hominid convergent with the lower facial pattern of *Gorilla*.

The Late Miocene

African Late Miocene hominoids are rare; they are represented by few remains, the majority of which have been unearthed only recently. A maxillary fragment of a large-sized hominoid from Kenya has been known since 1982; it is referred to as *Samburupithecus kiptalami* and dated to 9.5 Ma (Ishida and Pickford 1997). This sole known maxillary fragment has been claimed to have similarities with the modern gorilla by some researchers (Ishida and Pickford 1997), but others have recognized primitive *Proconsul* features and analyzed it as a survivor of *Proconsul* lineage during the Late Miocene (Begun 2007). The maxilla of *Samburupithecus* has some similarities to the Eurasian *Ouranopithecus*, such as the low origin of the zygomatic arches and the thick enamel; the taxon's relationships with the extinct and extant hominoids are unclear.

A mandibular fragment with extremely worn teeth, as well as some isolated teeth of a hominoid, have been described from Nakali, Kenya as the new species *Nakalipithecus nakayamae*, with an age of ~9.8 Ma; the Nakali material has strong similarities to *Ouranopithecus* and is considered a possible ancestor of the latter (Kunimatsu et al. 2007). The isolated canine of *Nakalipithecus* is similar to that of *Ouranopithecus*; likely an unworn M3 (KNM-NA46436) from Nakali is similar to that of *Ouranopithecus*, differing in the more developed buccal cingulum and the slightly smaller width. Except for geographic reasons, these small differences cannot support a different genus; even their age difference is very small and falls within the error range. More and better material from *Nakalipithecus* will be needed to clarify its relationships to the other Late Miocene hominoids.

Chororapithecus known from few isolated teeth from Ethiopia and dated to 10.5-10.0 Ma, is considered as is more closely related to African apes and the human clade than any Eurasian taxon. (Suwa et al. 2007). Although the last authors suggest similarity to the modern *Gorilla*, the material is very scanty for definite conclusions.

Some hominoid remains from the Latest Miocene of Africa (Fig. 3) provide more interesting data about the evolution of apes and hominines. A few mandibular and postcranial remains of a hominoid named *Orrorin* have been found in Kenya; the locality is dated at ~6.0 Ma (Senut et al. 2001). *Orrorin* is characterized by jugal teeth that are smaller than those of australopiths, a small dentition relative to body size, large and not shovel-like I1, short C, relatively deep mandibular corpus, and small M2 and M3 with thick enamel. The femur has a spherical head rotated anteriorly, an elongated neck with oval section, and a mesially salient lesser trochanter. The humerus has a vertical brachioradial crest, and the proximal manual phalanx is curved (Senut et al. 2001). *Orrorin* preserves some primitive ape characters (deep mandibular ramus, anterior teeth, and P4), as well as some more hominid ones (postcanine megadontia, postcranial pieces of evidence of bipedalism). According to Pickford et al. (2002), the femur of *Orrorin* shares some derived features with australopiths and *Homo*, but none with *Pan* or *Gorilla*, and among the Hominidae, it is closer to *Homo* than to australopiths.

In 2001, a skull with some mandibular and dental remains of a Late Miocene hominoid named *Sahelanthropus tchadensis* were found in Chad; the associated mammal fauna indicates a Latest Miocene age, 6.0–7.0 Ma (Brunet et al. 2002). The taxon is characterized by weak prognathism, a small braincase, a long and narrow basicranium, large canine fossa, a small and narrow U-shaped dental arch, a very wide interorbital distance, a thick and continuous supraorbital torus, relatively small incisors and canines, rounded cusps in the molars, and moderate enamel thickness (Brunet et al. 2002). *Sahelanthropus* exhibits several primitive features, like the small braincase, the morphology of the basioccipital bone, and the position of the petrous portion of the temporal bone. But it also preserves a set of derived features, such as small apically worn canines, medium-thick enamel, a horizontally oriented and anteriorly situated foramen magnum, reduced prognathism, a large and continuous supraorbital torus, and the absence of canine diastema, which indicate close relationship to the hominid clade. On the basis of the presence of this mosaic of characters and the age of *Sahelanthropus*, Brunet et al. (2002) suggested that it belongs to the hominid clade and is closer to the common ancestor of *Homo* and chimpanzees. Contrary to this opinion, Wolpoff et al. (2002) concluded that the dental, facial, and cranial characters of this skull cannot define its position among hominids.

The sparse material of both *Orrorin* and *Sahelanthropus* does not permit clear definition of their phylogenetic relationships with each other and with the other hominids. Given that there is little evidence for the presence of hominoids in the time interval from ~7.5 to 4.5 Ma, these two Late Miocene African hominoids constitute a link between the Miocene and Plio-Pleistocene hominids.

The Late Miocene Eurasian hominoids show impressive diversification and include the first indication of a relationship with the great apes and human clade. Different opinions have been expressed about their taxonomy and evolutionary relationships. They are classified with the pongines (Moyà-Solà and Köhler 1995, 1996), the dryopithecines (Casanovas-Vilar et al. 2011), and the hominines (Begun 2009, 2013) or, alternatively, as a dead group without relationship to the modern apes (Kunimatsu et al. 2007; Suwa et al. 2007).

The earliest known Late Miocene European hominoid is *Rudapithecus* from Rudabanya, Hungary, with an age of ~10.0 Ma (Kordos and Begun 2002). At the same time *Hispanopithecus* appeared in Spain (Casanovas-Vilar et al. 2011). Two skulls of *Rudapithecus* are known, which are characterized by a short face, an elongated neurocranium, weak but distinct supraorbital torus, biconvex vertically directed and relatively short premaxilla, narrow nasal aperture, high and broad root of the zygomatic arches situated above the mesial half of M2, shallow canine fossa, large interorbital distance, squared-to-rounded orbits, and a reduced foramen incisivum with short incisive canal (Kordos and Begun 1997, 2001). The cranial capacity of the Rudabànya skulls is estimated at a mean 320 cm^3 for RUD-77 and

305 cm^3 for RUD-197–200 (Kordos and Begun 1998, 2001). *Rudapithecus* shared a significant number of craniodental characters with the great apes and hominines (Begun et al. 2012; Table 1) and could be related to the ancestor of these groups. The postcranials of *Rudapithecus* preserve a mixture of characters between *Pongo* and the great apes. The humerus, ulna, femur, and phalanges are similar to those of the great apes, while the wrist bones have mixed pongine and great ape characters (Begun 1993; Begun and Kordos 2011).

Hispanopithecus is also known by a rich sample from the Vallesian of Spain (Fig. 3), including a partial face and skeleton (Moyà-Solà and Köhler 1995, 1996). The morphology of a lumbar vertebra suggests orthogrady, as in the modern great apes, while the femur and the phalanges are reminiscent of *Pongo* (Moyà-Solà and Köhler 1996; Almècija et al. 2007). Despite the mixed clues about their taxonomy, these early Late Miocene hominoids give strong indication of more affinities with the modern great apes and human clade than the Middle Miocene ones. They share several derived characters with the younger hominids and recent great apes, linking the Early Miocene African with the Late Miocene Eurasian hominoids.

A well-known hominoid from the eastern Mediterranean region is *Ouranopithecus*, which is represented by the two species *O. macedoniensis* and *O. turkae*, while one P4 from Bulgaria also bears strong similarities to this genus (de Bonis et al. 1973; 1990; de Bonis and Koufos 1993, Koufos and de Bonis 2004; Koufos 1993, 1995; Güleç et al. 2007; Spassov et al. 2012). The type species *O. macedoniensis* is known from three localities in northern Greece by numerous craniodental remains. All localities are correlated to the Late Vallesian or to European Mammal Zone MN 10. The bio- and magneto-chronology suggest an age between 9.6 and 8.7 Ma (Koufos 2006, 2013).

O. macedoniensis has a large body size, in the range of variation of gorillas. There is strong sexual dimorphism expressed in the overall size of the dentition and in the size and morphology of the canines. In brief, the morphological characters of *O. macedoniensis* (Fig. 6) are as follows: a well-developed supraorbital torus with a small glabellar depression, large interorbital distance, relatively short nasals, small, low, and quadrangular orbits, primitive nasoalveolar area with a large fossa incisiva, strong and low-rooted zygomatic arches, narrow and convex mandibular condyle, low and thick horizontal ramus, long planum alveolare with well-developed fossa genioglossa, strong superior and inferior torus, shovel-like incisors, relatively reduced canines, relatively symmetric upper premolars, low cusps in the molars, more symmetric P3 without honing facet, thick enamel, and an absent or very weak cingulum (de Bonis and Melentis 1977, 1978, 1985; de Bonis and Koufos 1993; Koufos 1993, 1995; de Bonis et al. 1998; Koufos and de Bonis 2004). The species is a hard-object feeder (Merceron et al. 2005, 2007), living in an open environment with shrubs, bushes, and small trees, and thick grass floor such as savanna woodland (de Bonis et al. 1992, 1999; Koufos 1980, 2006).

The phylogenetic position of *O. macedoniensis* among the hominids is very important, as it shares several derived characters with *Australopithecus* and *Homo*. Some of these characters are discussed in more detail below.

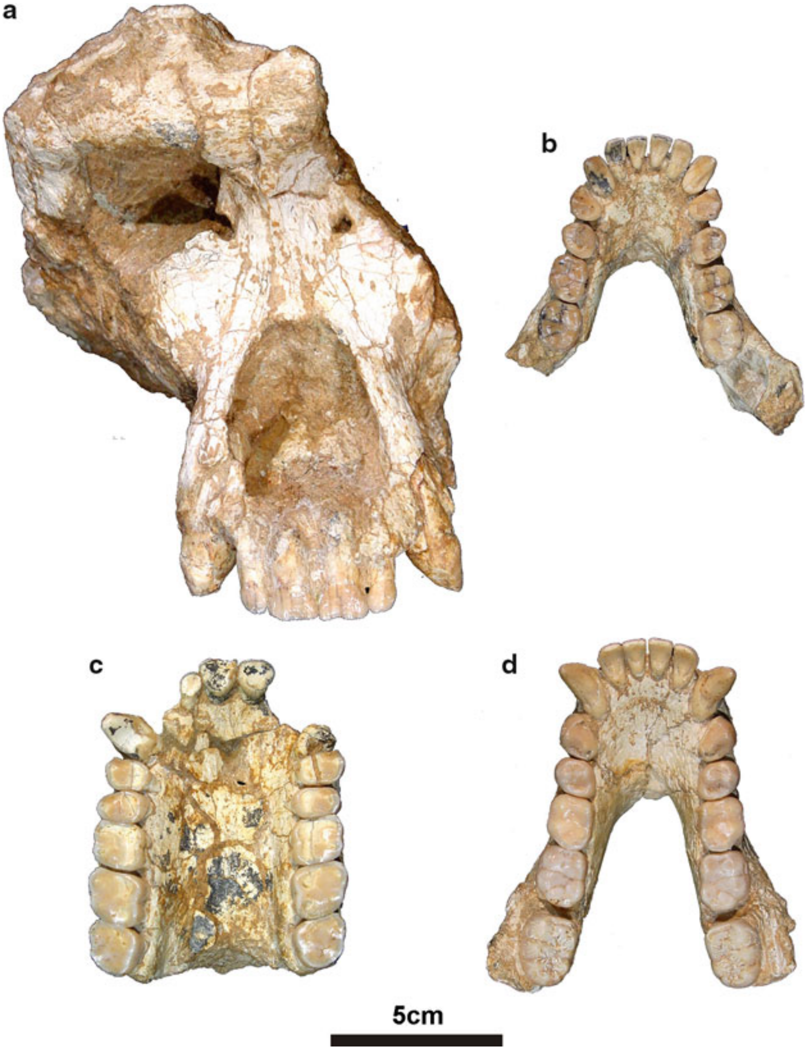

Fig. 6 *Ouranopithecus macedoniensis*, Axios Valley, Macedonia, Greece. (**a**) Male skull from Xirochori-1, XIR-1; (**b**) female mandible from Ravin de la Pluie, RPl-54, HOLOTYPE; (**c**) male maxilla from Ravin de la Pluie, RPl-128; (**d**) male mandible from Ravin de la Pluie, RPl-55

The lateral outline of the upper face is a derived character, since in primitive Early–Middle Miocene hominoids it was more oblique, while in *O. macedoniensis* it is more vertical. The glabella–nasion–prosthion angle is 120°, while in the fossil and extant apes it reaches 140°. In *Australopithecus africanus* it is 115° and in *A. boisei* 150°, because of the flattening of the face (de Bonis and Koufos 1993).

The structure of the naso-alveolar area of *O. macedoniensis* belongs to the primitive "African pattern," as also seen in *Dryopithecus* and *Gorilla*. It is different from that of *Pongo* and *Sivapithecus*, while it is closer to *Australopithecus* (de Bonis and Melentis 1987; de Bonis and Koufos 1994). However, it is more derived than *Proconsul* and *Morotopithecus* and less derived than *Australopithecus afarensis* and the recent chimpanzee.

The narrow mandibular condyle of *O. macedoniensis* is a more hominine-like character. In the apes, the mandibular condyle is only slightly convex, while in *Homo* it is narrower and more convex. In *A. afarensis* it is more apelike (de Bonis and Koufos 1997, 2001). The narrowness of the mandibular condyle can be measured by the index [cranial–caudal diameter × 100/medial–lateral diameter]. In *O. macedoniensis* this index is 44.4, in *A. robustus* 33.8, in modern *Homo* 41.4–45.7, in *Gorilla* 46–56, in *Pan* 47–53, and in *Pongo* 43.3–43.9 (de Bonis and Koufos 1993). Both the narrowness and the shape of the mandibular condyle are related to the form of the temporomandibular joint. The latter is large and relatively flat in apes, while in hominines its anterior part is cylindrical and followed by a mediolateral directed fossa (Picq 1990). The capitulum of the *O. macedoniensis* mandible could correspond to the latter kind of temporomandibular joint.

The cingulum is absent or very weak in all cheek teeth of *O. macedoniensis*; compared to the strong cingula of *Proconsul* and the pliopithecids; this is a derived character. The presence of accessory cusps (cuspids) at the distal ends of the upper and lower third molars, as in *Australopithecus afarensis*, is a derived character for *O. macedoniensis* – one that is related to the function of the teeth. The enamel thickness relative to the body weight of *O. macedoniensis* can be compared to that of some australopiths (*Paranthropus*, *Australopithecus africanus*),but it is thicker than in *Dryopithecus*, *Sivapithecus*, *Proconsul africanus, P. major, Gorilla, Pan*, and *Pongo* (de Bonis and Koufos 2001). Thus, enamel thickness could be a primitive feature relative to the recent hominoids, but derived when compared to the Early–Middle Miocene hominoids. Enamel thickness depends also upon the hardness of the food. A change to a more open environment, such as woodland or wooded savanna, is associated with harder food items. In the eastern Mediterranean an environmental change which brought about more open habitats occurred at the end of the Middle Miocene (Koufos 2006), leading to thick enamel in hominoids like *Ouranopithecus* and *Ankarapithecus*. At the same time, in western and central Europe the environment continued to be more forested (until the Middle Vallesian), and correspondingly the hominoids from those regions are thin-enameled (*Dryopithecus, Rudapithecus*).

The morphology of the P3 in *O. macedoniensis* (not elongated, rounded occlusal outline, more symmetric buccal face, absence of a honing facet, less oblique protocristid) distinguishes it from the apes. The wear pattern of the crown in the P3 is similar to that in *Australopithecus afarensis*, as a result of the absence of a honing facet in both forms and the similar function of the tooth (de Bonis and Koufos 2001). Indeed, the wear pattern of the whole dentition of *O. macedoniensis* is similar to that of *A. afarensis* (Koufos and de Bonis 2006).

The size of the upper canine of *O. macedoniensis* is a derived character. The plesiomorphic characters of the canine are the high, buccolingually flattened crown and the presence of a sharp distal crest on the buccolingual surface. This feature is present in cercopithecids, as well as in extant and Early–Middle Miocene hominoids. The shape of the canine is more rounded and in this respect very close to *Australopithecus afarensis*. The height of the upper canine of *O. macedoniensis* is relatively reduced (de Bonis and Koufos 1993), while its morphology is completely different from that of the primitive hominids. The height of the crown is less reduced than in *Australopithecus afarensis* (Johanson et al. 1982). In comparison, the canine of *Proconsul* is three times larger than that of *O. macedoniensis*. The size of the canine compared to the size of the cheek teeth is also small in *O. macedoniensis*, and is similar to that in *Australopithecus afarensis* and female *Gorilla*. It is much larger (more than 120) in the Early–Middle Miocene and extant hominoids (de Bonis and Koufos 1993).

In regards to the lower deciduous dentition, *O. macedoniensis* shares some derived characters with the Plio-Pleistocene hominines. The deciduous canine of *O. macedoniensis* is more reduced, compared to the molars, than that of *Proconsul* and *Ardipithecus*, but less reduced than that of australopiths and *Homo*. The lower deciduous premolars of *O. macedoniensis* are more derived than in Early–Middle Miocene and recent hominoids, and less derived than in australopiths and *Homo* (Koufos and de Bonis 2004).

All of these characters suggest that *O. macedoniensis* has strong relationships to the Plio-Pleistocene hominines: it shares several derived characters with them and can be considered their ancestor. A cladistic analysis of 22 derived characters of *O. macedoniensis* shared with the extinct and extant hominoids, as well as with *Australopithecus* and *Homo*, suggests that (i) *O. macedoniensis* can be included in the subfamily Homininae; (ii) the splitting of *Homo* and the African apes is dated at more than 9.5 Ma; and (iii) *O. macedoniensis* can be considered a sister group to *Australopithecus* and *Homo* (de Bonis and Koufos 1997).

Ouranopithecus macedoniensis also has several characters similar to those of australopiths; some of them are plesiomorphic (shape of symphysis, large interorbital distance, shallow or absent supratoral sulcus, large M3, development of nasomaxillary area). However, it preserves a set of apomorphic features. Some of them, such as thick-enameled teeth or canine reduction, may be homoplasies, but it would be peculiar and exceptional for all of them to be homoplasies (de Bonis and Koufos 1999). There are some differences of opinion concerning this hypothesis. Begun (1992) suggests a relationship between *Gorilla* and *O. macedoniensis* and concludes that *Dryopithecus* has slightly more evidence (gnathic structures and positional behavior) in its favor for being ancestral to African apes and humans. But the postcranial morphology, and consequently the positional behavior of *O. macedoniensis*, are unknown. The two available phalanges of *O. macedoniensis* are different from those of all arboreal primates and closer to terrestrial forms. Begun (2002, p. 365) states that “it is not clear which taxon, *Dryopithecus* or *Ouranopithecus*, comes closer to the ancestral morphology of the African apes and humans”. Although he gives a slight precedence to *Dryopithecus*, he refers that the unknown positional behavior of *Ouranopithecus* is a disadvantage. Begun subsequently links *O. macedoniensis* with the dryopithecines (*Dryopithecus*, *Hispanopithecus*, *Rudapithecus*) “as a group that is the sister clade to African apes and humans" (Begun 2009). Earlier, Andrews et al. (1996) made the statement that *O. macedoniensis* "is recognized as a hominine, related to the African ape and human clade and possibly close to the ancestry of the living species of this group." In their phylogeny of the Hominoidea, *O. macedoniensis* is the possible ancestor of the gorilla, chimpanzee, and humans (Andrews et al. 1996, Fig. 12-7). Benefit and McCrossin (1995) considered *O. macedoniensis* to be linked with the African ape and human clade, because of the presence of a supraorbital torus and the rectangular orbits. They also link *Samburupithecus* with *Ouranopithecus*, suggesting that the former may be a potential candidate for membership in the African ape and human clade. However, the dental morphology of *Samburupithecus* differs from that of *Ouranopithecus* in having more voluminous and higher cusps. Recently Clarke (2012, p. 45) noted that "the one Miocene ape that does show remarkable dental similarity to the early hominid *Australopithecus* is *Graecopithecus-Ouranopithecus macedoniensis*."

The first edition of this handbook (Koufos 2007, p. 23), in discussing the phylogenetic position of *O. macedoniensis* and the various opinions about it, stated: "But Africa is a huge region and who knows what will be discovered in the future." Indeed, two new articles, published in the same year, described new Late Miocene hominoid material from Kenya and Ethiopia (Kunimatsu et al. 2007; Suwa et al. 2007). Despite the poor material, both samples have similarities to *O. macedoniensis*, especially *Nakalipithecus*, and might belong to the subtribe Ouranopithecina of Begun (2009), linking the Late Miocene African and Eurasian hominoids.

Ouranopithecus turkae is a new species found in Turkey (Güleç et al. 2007); together with the sole P4 from Bulgaria (Spassov et al. 2012) they represent the Turolian evidence for hominoids in Eurasia. Its classification as *Ouranopithecus* has been questioned (Begun 2009), although it does have similarities with this genus, as well as with *Indopithecus* (Begun 2013).

Another Asian Late Miocene hominoid is *Ankarapithecus*, found at Sinap Tepe (Turkey) and known from three cranial remains. This hominoid is dated at ~10.0 Ma (Kappelman et al. 2003) and seems to be slightly older than *Ouranopithecus*. It was interpreted as having relationships with hominids (Alpagut et al. 1996), but recent analysis indicates phylogenetic relationships with the *Sivapithecus–Pongo* clade based on shared characters (massive maxilla, broad nasal aperture, high-placed zygomatic arches, narrow interorbital distance, very elongated nasal bones, absence of real supraorbital tori) (Begun and Güleç 1998). Thus, *Ankarapithecus* seems to be closely related to *Sivapithecus* and recent *Pongo* or to the Asian hominoids.

Oreopithecus is known from Italy only, where it has been found at the localities of Bacinello, Casteani, Ribolla, Montebamboli, and Fiume Santo and is in each case associated with an endemic fauna (Rook et al. 1999). The localities have been dated to the Middle–Late Turolian (Late Miocene), or at about 6.0–7.0 Ma (Harrison and Rook 1997; Steininger 1999). *Oreopithecus* is known by numerous cranial and postcranial remains, including a complete skeleton. It can be considered the best-represented European Late Miocene hominoid.

The very small braincase, low zygomatic root, short and gracile premaxilla, long and narrow palate, narrow nasal cavity, projecting midface, and relatively high canines of *Oreopithecus* are primitive features distinguishing it from all great apes (Begun et al. 1997; Harrison and Rook 1997). The postcranial morphology of *Oreopithecus* resembles that of the hylobatids and is related to suspensory positional behavior. It is also similar to that of the hominids and is related to large body mass in suspensory quadrupeds, with powerful grasping and high joint mobility (Harrison and Rook 1997). The majority of the morphological characters of *Oreopithecus* indicate that it is the most primitive known great ape (Harrison 1986b; Harrison and Rook 1997). Nevertheless, some researchers instead consider it a highly derived member of the clade including all Eurasian Late Miocene hominoids (Moyà-Solà and Köhler 1995, 1997) and is situated at the base of the hominoid radiation representing ancestral hominid morphology (Harrison and Rook 1997; Begun 2002). However, it is necessary to keep in mind that *Oreopithecus* belongs to an endemic fauna and that some of its characters may be secondary adaptations to the local conditions.

There are a number of Asian hominoids, like *Sivapithecus*, *Indopithecus*, *Khoratpithecus*, and *Gigantopithecus* (Andrews et al. 1996; Kelley 2002; Chaimanee et al. 2006; Jaeger et al. 2011), which are known from ~12.0–7.0 Ma. All these hominoids have strong relationships with the modern orangutan and are related to the *Pongo* clade. Besides the Middle Miocene *Griphopithecus* and *Kenyapithecus* and the late Miocene *Ouranopithecus*, there is another Asian hominoid, *Udabnopithecus garedziensis* from Georgia. The known material includes two molars; *Udabnopithecus* is somewhat confusingly classified either as *Dryopithecus* (Andrews et al. 1996; Gabunia et al. 2001) or under its original name (Lordkipanidze et al. 2008). The concentration in the most western part of Asia of these Middle–Late Miocene hominoids that are related to the great apes and the human clade, while in the rest of the continent only pongines have been found, indicates that Asia Minor was a migration route from Africa to Eurasia and vice versa.

Conclusion

The ancestor of the hominids and recent great apes is included in the stem of the Miocene hominoids, the common stock of hominids and apes. Despite the great expansion of the hominoid fossil record during the last decades, that fossil record is still quite poor and limits analysis and conclusions. From millions of hominoids that lived for a long time (∼20 Ma), only very few and fragmentary remains are available, based on which scientists are trying to complete the chain of hominid evolution link by link. The absence of some links makes their work more difficult, and at times even the discovery of a possible link may cause more problems than it solves. The limited conclusions we can draw based on recent data and known material include the following:

- Oligocene *Aegyptopithecus* and *Kamoyapithecus* could be the possible ancestor of the Miocene hominoids, as they share some derived features with the early hominoids. However, the large time gap between these taxa, and between them and the first proconsulids, is a source of uncertainty.
- Among the Early Miocene hominoids, *Proconsul* is the most plausible link connecting the hominoids to the modern great apes and the hominines. Controversy over particulars notwithstanding, it can be said to display a mosaic of features that indicate relations to the extant great apes and humans. Several other hominoid taxa known from the Early Miocene might also represent the sought-after link; but their limited and fragmentary material prevents definite comparisons and results.
- The Middle Miocene hominoids of Europe seem to be an important group, which could include a possible link. Certain Middle Miocene hominoids from Africa could also represent a link, but their poor material does not allow reliable comparisons, and their relationships to other taxa are still being discussed.
- The overall cranial and dental morphology of *Ouranopithecus* seems to be closer to the hominids; possibly it is this taxon that constitutes the Late Miocene link connecting the hominoids to the extant great apes and humans – either as a sister group to *Australopithecus* and *Homo* (de Bonis and Koufos 1997) or as a sister clade to the African apes and humans (Begun 2009).
- The similarities of *Sahelanthropus* and *Ouranopithecus* (Brunet et al. 2002) indicate a close relationship between them, narrowing the gap between *Ouaranopithecus* and *Australopithecus*.
- All known Asian hominoids, such as *Sivapithecus*, *Indopithecus*, *Ankarapithecus*, *Khoratpithecus*, and *Lufengpithecus*, are closely related to the modern orangutans.

The question of human origin will preoccupy scientists for a long time. Each new discovery will add further data, but will also raise new questions and possibly controversies. Despite these challenges, it is very important that scientists continue their effort to collect more material and study all fossil and modern hominoids in systematic detail, in order to better understand their evolutionary relationships. Continued research efforts and the development of new methods will bring us ever closer to a full understanding of human origins.

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Cross-References

▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition
▶ Fossil Record of Miocene Hominoids
▶ Hominoid Cranial Diversity and Adaptation

- ▶ Origin of Bipedal Locomotion
- ▶ Postcranial and Locomotor Adaptations of Hominoids
- ▶ Primate Life Histories
- ▶ Primate Origins and Supraordinal Relationships: Morphological Evidence
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ The Species and Diversity of Australopiths

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Defining Hominidae

Jeffrey H. Schwartz

Contents

Abstract

A array of relevant cranial, postcranial, and dental morphologies are reviewed in an attempt to delineate shared derived features that would unite a group that includes extant humans and their fossil relatives to the exclusion of other hominoids. This group is now often referred to as tribe Hominini, but systematic practicality suggests that family Hominidae be retained, since the lower rank de facto limits even current, and certainly future, recognition of subclades. Potential hominid postcranial synapomorphies include a distinct angle at L5–S1, a long pubic ramus, a superoinferiorly short ilium that is roundedly expanded posteriorly, some thickening in the region of an iliac (crest) tubercle, a well-developed and

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J.H. Schwartz (✉)
Departments of Anthropology and History and Philosophy of Science, University of Pittsburgh, Pittsburgh, PA, USA
e-mail: jhs@pitt.edu

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knoblike anterior inferior iliac spine that lies noticeably superior to and somewhat back over the superior acetabular rim, a defined and deep greater sciatic notch, differential distribution of cortical bone of the femoral neck, anteroposteriorly long femoral condyles, and an outwardly slanted femoral shaft. Although "a weakly defined linea aspera" and "a concave rather than convex medial tibial condylar facet that lies level with the primitively concave lateral facet with the two facets being separated by a pair of distinct tibial tubercles" have been suggested as hominid apomorphies, this appears not to be the case – unless the apelike specimens commonly taken as hominid (e.g., from Hadar) are not. The only possible cranial feature appears to be alignment in the adult of the biporionic chord and basion (on the anterior margin of the foramen magnum). Derived dental features that might unite Hominidae also characterize an orangutan clade and thus must be explained away (e.g., as homoplasies) or dismissed as phylogenetically relevant in order to justify the former group. Of further note is the presence of *Pongo* clade-like facial features in australopiths and various specimens of *Homo*. These and the dental similarities suggest that focusing on *Pan* alone as the out-group from which to judge hominid-defining features is comparatively too narrow and, consequently, phylogenetically misleading. Within Hominidae, various subclades can be justified, suggesting that the relationships of various specimens referred to genus *Homo* lie within a clade that also subsumes "australopiths." Much work remains before clade Hominidae can be more fully defined.

Introduction

By the twenty-first century, one would think that paleoanthropology would long ago have left behind the legacy of Linnaeus' (1735) ultra-vague and systematically useless definition of our species, *Homo sapiens*: nosce te ipsum (know thyself). Yet, in spite of the incredible number of discoveries of fossils attributed to our clade (i.e., the clade that includes *H. sapiens* but excludes apes) since the mid-to-late nineteenth century – when discovery of the Feldhofer Grotto Neanderthal and ultimately the Spy Neanderthals undermined the notion that humans were not antediluvian – the history of paleoanthropology contrasts with that of the centuries-old disciplines of vertebrate and invertebrate paleontology in its increasing rejection of taxonomic and systematic rigor. Consequently, the task of defining Hominidae is not as straightforward as one might imagine it should be.

Historical Background

In the first detailed attempt to support Linnaeus' inclusion of humans within a specific group of mammals, and particularly in grouping humans with apes, Thomas Henry Huxley (1863b) sought evidence of this relationship not only in comparative hard- and some soft-tissue morphology but also in comparative development. Through ontogenetic comparison, he argued that if a monkey could be distinguished developmentally from other vertebrates as a mammal generally, and a primate more specifically, so, too, could humans. Hence, if a monkey was a primate, so, too, was a human. Huxley then turned to "man's place in nature" within Primates. He began with the premise that humans were most similar to gorillas and then organized his comparisons first between gorillas and, when needed, other apes and then between them and monkeys. His rationale was if a morphological "gulf" existed between gorillas and monkeys, but not between gorillas and other apes, then humans could also be allied with the apes. But while Linnaeus claimed that, in essence, morphology barely distinguished humans from apes (Schwartz 1999), Huxley believed otherwise. Consequently, in spite of demonstrating that anatomies as distinctive as the human foot were basically comparable to the grasping feet of apes and monkeys, Huxley concluded that humans were still sufficiently unique to warrant their own taxonomic status apart from the great apes, all of which he relegated to a separate family. In hard-tissue morphology, Huxley remained as impressed by aspects of the postcranial skeleton as Aristotle had been of the human thumb and Johann Friedrich Blumenbach of the human pelvic girdle and foot.

With his emphasis on aspects of the human postcranium and dentition, Blumenbach should be regarded as the "father of paleoanthropology" inasmuch as the criteria he used to distinguish humans from other animals eventually became those that paleoanthropologists used to decide if a fossil qualified as a "hominid" (Schwartz 1999). Indeed, in 1795, in *On the Difference of Man from Other Animals*, Blumenbach (1969) emphasized various aspects of "the external conformation of the human body" as paramount to defining *Homo sapiens*: erect posture, broad and flat pelvis, two hands, non-divergent hallux, close-set and serially related anterior teeth, and some aspects of mandibular morphology.

With regard to erect posture, Blumenbach argued that, in contrast to other animals, this stance was natural and specific to *H. sapiens* as noted, for instance, in the ossification of tarsals before carpals. He claimed that only humans have a "true" pelvis, in which the broad and expanded ilia form a basin that cups the viscera. Like Aristotle, he regarded the human hand as special because of its long thumb. In addition, because of the uniqueness of the human foot, with its non-divergent hallux, Blumenbach believed that possession of only two "true" hands was significant. He also considered the human dentition distinctive in presenting orthally implanted lower incisors; canines not longer than, or separated from, the incisors; and molars with rounded cusps. He described the human mandible as quite short, bearing a prominent chin, and having a distinctive articulation with the skull (presumably referring to the depth of the articular fossa), which, he suggested, was correlated with human omnivory.

Although he recognized that humans differ from many mammals in lacking a distinct premaxilla, Blumenbach also, but mistakenly, believed that other primates were similar in this regard – a claim he then used to argue against separating humans from other primates taxonomically. [Goethe (1820) made a similar argument but did so on the incorrect belief that he could identify a premaxilla in humans.]

In addition to "the external conformation of the body," and in keeping with concerns of eighteenth-century philosophers, Blumenbach (as well as Goethe) addressed the "internal conformation" of humans, i.e., the importance of reasoning (as well as other mental attributes) as a criterion by which to distinguish humans from other animals, including other primates. Although not stated in these terms, we might point to a focus on mental attributes as underlying the later emphasis in paleoanthropology on the size and external morphology of the brain [features that also attracted the attention of the eighteenth-century naturalists Buffon and Bonaparte (Schwartz 1987)].

Blumenbach's criteria for distinguishing humans from other animals were imported into paleoanthropology with the discovery of *Homo* (*Pithecanthropus*) *erectus* from Trinil, Indonesia (Schwartz 1999). This historical twist is likely due to Huxley's (1863a) argument that the Feldhofer Grotto Neanderthal was an extinct human whose cranial features extended into the past a "perceived" continuum of racial "brutishness" from the most "civilized" to the most "brutish" of living humans. In turn, these notions of ancientness equating with primitiveness and of a continuum that proceeded from a brutish primitiveness to human modernity came to inform much of paleoanthropology (Schwartz 1999).

The Trinil specimens, however, undermined Blumenbach's *H. sapiens*-defining criteria. While the femur provided evidence of humanlike bipedalism (Blumenbach's "erect posture"), the skullcap depicted an individual that had been less than fully human in its brain (and thus in its mental capacities). This unexpected combination of human and less-than-human features prompted Dubois to assign his new *erectus* first to the genus *Anthropopithecus* (the taxonomic alternative to *Pan*) (Dubois 1892) and then to Haeckel's proposed genus for a hypothetical extinct, speechless human relative, *Pithecanthropus* (="ape-man") (Dubois 1894). The implication, of course, was that the emergence of erect posture and bipedalism preceded expansion and elaboration of the brain.

While lending itself to Darwin's (1871) suggestion of a smooth transition from a semi-quadrupedal African ape to an erect bipedal human, this picture – bipedalism first, brain second – appeared contradicted with the discovery in the early 1900s at Piltdown, England, of a large, thin-boned, and rounded humanlike cranium; an apelike partial mandible preserving two molars; and an apelike lower canine. Under the presumption that these specimens were associated, the Trinil-based scenario of human evolution was turned around: early human relatives became human first in their brains and then in the rest of the body (as inferred from the mandible and teeth). That is, the brain enlarged prior to the attainment of fully erect posture and bipedal locomotion. It was not until the 1950s, when the Piltdown fraud was exposed, that this alternative notion of human evolution – brain first, body second – was rejected. Before then, however, the discovery of the Taung child and, more importantly, Dart's (1925) interpretation of the specimen continued the intellectual trajectory Blumenbach had begun. But Dart conceived his scenario in the context of Darwin's incorrect biogeographic premise of finding fossil evidence in Africa of intermediate forms that provided evidence of a morphological continuum between African apes and humans.

As Dart (1925, p. 196) summarized his overall impression of the preserved craniodental features of the Taung specimen, this individual represented "an extinct race of apes *intermediate between living anthropoids and man*." Dart depicted specific features – such as the configurations of the brow, nasal bones, zygomatic regions, orbits, and upper and lower jaws as well as the inferred skull shape – as being of "delicate and humanoid character" (Dart 1925). Most central to his speculations were the size and potential details of the preserved partial endocast and also the forward position of the foramen magnum (as indicated by bone adherent to the endocast). Dart (1925, p. 197) assumed the latter was proof of this "humanoid's" erect posture and then made the following extrapolations:

> The improved poise of the head, and the better posture of the whole body framework which accompanied this alteration in the angle at which its dominant member was supported, is of great significance. It means that a greater reliance was being placed by this group upon the feet as organs of progression, and that the hands were being freed from their more primitive function of accessory organs of locomotion. Bipedal animals, their hands were assuming a higher evolutionary rôle not only as delicate tactual, examining organs which were adding copiously to the animal's knowledge of its physical environment, but also as instruments of the growing intelligence in carrying out more elaborate, purposeful, and skilled movements, and as organs of offence and "defence". The latter is rendered the more probable, in view, first of their failure to develop massive canines and hideous features, and secondly, of the fact that even living baboons and anthropoid apes can and do use sticks and stones as implements and as weapons of offence.

Regarding the Taung child's brain (as represented by the endocast), Dart suggested that, since it was already as large as a chimpanzee's and almost as large as a gorilla's, it would have continued to enlarge, following a humanlike growth curve. In addition, as in humans but not apes, the Taung child's brain was high and rounded, somewhat expanded in the temporal region, and apparently a posteriorly and inferiorly placed lunate sulcus. Believing his specimen to be more human- than apelike, Dart inferred that this "humanoid" had also been humanlike in its faculties of "associative memory and intelligent activity." The expanded cerebral cortex (as indicated by the presumed lunate sulcus) also suggested to Dart that, in contrast to apes, the Taung "humanoid" had experienced increased sensory stimulation, both via vision (because of the forward position of the approximated orbits) and tactile sensation (because erect posture and bipedality supposedly freed the hands from involvement in locomotion). But the Taung child's brain was not sufficiently enlarged in the temporal region for it to have reached the "necessary milestone in the acquisition of articulate speech" (Dart 1925, p. 198).

For Dart, the Taung child, the name bearer of his genus and species *Australopithecus africanus*, displaced both Piltdown's *Eoanthropus dawsoni* and Trinil's *Pithecanthropus erectus* as viable "links" between humans and their apelike ancestors. Indeed, in spite of Dart's conceiving this extinct juvenile as intermediate between humans and apes, his interpretation reflected Blumenbach's criteria for distinguishing *Homo sapiens*. In 1925, then, in spite of their differences, the three scenarios regarding human ancestry embraced the notion of an evolutionary continuum that proceeded from an apelike precursor, through an unknown series of intermediates, to the most modern looking of living humans.

In terms of the focus of this chapter – defining Hominidae – subsequent discoveries of potential extinct human relatives are less relevant than attempts to integrate these fossils into a systematic framework that had originally been based on living *Homo sapiens*. In this regard, after a decade-and-a-half of successful fossil hunting in the limestone caves of South Africa and in caves and deposits in Europe and Asia, and a proliferation of genus and species names, and debates over the relationships of what I will refer to as "australopiths" (based initially on South African specimens), Le Gros Clark (1940) was compelled to review the available evidence in order to determine the hominid status of any australopith.

In addition to echoing Huxley and Darwin's assumption of a linear transformation from ape to human, Le Gros Clark based his conclusions on what he later called the "total morphological pattern" (Le Gros Clark 1955). From this perspective, he considered a fossil as being hominid not in terms of derived features it shared with humans but whether, overall, it resembled humans more than great apes. As will become obvious, this approach complicated matters further because the great apes were then considered evolutionarily united. Thus, a feature to compare with humans or potential hominid fossils could be extracted from any ape and deemed exemplary of the entire group, even if it only characterized the one ape [Gregory (1922) employed this device of "pick and choose" in arguing for an African ape-human relationship (Schwartz 2005)]. The irony of Le Gros Clark's phenetic approach is that in 1955 he made one of the clearest statements about distinguishing between primitive and derived characters in generating hypotheses of relatedness.

Although Le Gros Clark (1940, p. 317) concluded that australopiths were "more human than simian" especially in their teeth, his comparisons then and in subsequent publications were biased toward the African taxa. If, however, he had included *Pongo*, he might have been struck by the similarities between this hominoid and australopiths in many details of facial and dental morphology (Schwartz 2004a, 2005). Perhaps then he might have expanded his comparisons to include at least small-bodied hominoids and some Old World monkeys, thereby providing paleoanthropology with the precedent of a more broad-based approach to phylogenetic reconstruction. Unfortunately, he did not, thus making his efforts to define Hominidae as useless as his definition of the order Primates [i.e., being characterized by their lack rather than sharing of derived feature/s (Le Gros Clark 1959)].

Mayr's (1950) influential article on fossil hominids did not clarify the situation. Rather, on the grounds that all hominids were adaptively similar because they were bipedal, Mayr collapsed all named taxa into one genus, *Homo*. After claiming that because living humans are so diverse and occupy all available econiches the same had been true for all hominids (thus precluding the opportunity and prerequisite for speciation) (Mayr 1963), he subdivided his genus *Homo* into three time-sequential species: *transvaalensis*, *erectus*, and *sapiens*. Even though a much enlarged human fossil record later provoked Mayr (1953) to "accept" *Australopithecus* and acknowledge also *Paranthropus*, but as side branches that went extinct without issue, his concession did not elucidate how one determined in the first place if a specimen was hominid, especially if postcranial remains were unknown. This is, indeed, a problem. For while it may be true that some scholars (e.g., Le Gros Clark, Mayr, Washburn) decided "that the most important single factor in the evolutionary emergence of the Hominidae as a separate and independent line of development was related to the specialized functions of erect bipedal locomotion" (Le Gros Clark 1964, p. 14), the preponderance in the human fossil record of usually fragmentary skulls and jaws and isolated teeth makes impossible identifying a specimen as "hominid" on the basis of anatomical features believed to be reflective of bipedal locomotion. The cranial exception, of course, is the region of the foramen magnum and occipital condyles.

Toward a Definition of Hominidae

The task of defining Hominidae is twofold. First is a taxonomic decision. How expansive is the classificatory net Hominidae? To chimpanzees? Chimpanzees and gorillas? All great apes? Although Le Gros Clark (1955, 1964) wrote at a time when all great apes were relegated to the taxonomic family, Pongidae, his rationale for recognizing family Hominidae is, I believe, still viable and useful. Namely, Hominidae is a monophyletic group that subsumes extant humans and their fossil relatives, to the exclusion of any living relative. (It is in this sense that I use Hominidae/hominid/hominids throughout this contribution.) Accepting this proposition does not impinge on one's preferred version of ape as closest living human relative. Further, it also allows more systematic space in which to accommodate the still taxonomically expanding human fossil record – which collapsing *Pan* and all hominids into genus *Homo*, on the grounds that this is "cladistic" (Goldberg et al. 2003), obviates. Indeed, the only thing "cladistic" about this, in the spirit of Hennig (1966), is translating a preferred scheme of relationship directly into a classificatory representation of it – which is not the same as generating the theory of relationship.

With this suggestion in mind, we can turn to the matter of defining Hominidae, but not from the perspective of looking for the "defining" moment in a transition from a presumed apelike condition to something seemingly hominid (either by a subtle hint of a supposed hominid trait or traces of a presumably primitive and retained feature). Rather, it seems logical and reasonable to return to Blumenbach's list of criteria, to which other features have been added, as defining a clade that includes humans and their extinct relatives.

Defining Characters of Hominidae?

Traditionally Accepted Features of "Erect Posture"

As reviewed above, Blumenbach's emphasis on "erect posture" and "two handedness" – or, as Le Gros Clark (1964, p. 14) put it, on "specialized functions of erect bipedal locomotion" – has remained central to considerations of our clade. Pilbeam (1972, p. 62), for example, summarized some of the "adaptations" apparently associated with these "specialized functions of erect bipedal locomotion": a vertebral column with a distinct lumbar curve that is set at a sharp angle relative to the sacrum; a "carrying angle," wherein the lateral femoral condyle is larger and more weight bearing than the medial condyle and the femoral shaft angles up and laterally away from the knee joint; a non-grasping foot with short toes and non-divergent hallux through which weight is transmitted during locomotion; and metacarpals in which the heads contact the substrate while the distal ends are elevated to form a springlike, transverse arch. We might also include Blumenbach's description of the pelvic region as bowl shaped (i.e., broad and shallow) and having a short, potentially laterally flaring, posteriorly expanded, anteriorly truncated ilium; a somewhat forwardly oriented acetabulum (which is also reflected in the orientation of the proximal femur relative to the shaft); a defined greater sciatic notch; and a broad, short sacrum, wherein the alae are not remarkably small relative to the size of the lumbar facet (Schultz 1968). Clearly, these features distinguish living *Homo sapiens* from other extant primates. However, the degree to which these characteristics are expressed in what have been identified as fossil hominids, and whether the appropriate postcranial remains are known, is still up for debate.

For instance, among fossil specimens attributed to "anatomically modern" *Homo sapiens* that probably represent this taxon (Schwartz and Tattersall 2000a, b; Schwartz and Tattersall 2003, 2010), only Qafzeh 9 is known from a fairly complete, albeit extremely crushed, postcranium. Inasmuch as distortion of its skull and mandible compromises definitive identification of a bipartite brow with a "glabellar butterfly" and a mandible with a "true" chin with an inverted "T" configuration and thickened inferior symphyseal margin (Schwartz and Tattersall 2000a, b; Schwartz and Tattersall 2003, 2010), the pelvic region appears to present *H. sapiens*, not Neanderthal, morphology (Rak 1990) (personal observation). Other cranial and/or mandibular specimens conventionally attributed to "anatomically modern" *H. sapiens* and preserving critical morphology, especially Qafzeh 6 and all from Skhūl, do not present a bipartite brow or an inverted mandibular symphyseal "T" (Schwartz and Tattersall 2000a, b). Known Skhūl postcranial remains are incompletely representative and so crushed and poorly reconstructed that one can only sense their conforming to the abovementioned pelvic configurations (personal observations).

While Neanderthal postcranial morphology associated with bipedal locomotion differs from *Homo sapiens* in details of size, shape, and morphology [e.g., more posteriorly expanded ilia, superoinferiorly tall and anteroposteriorly compressed pubic symphyseal region, relatively long pubic ramus (and thus very wide/obtuse subpubic angle), smoothly "hook-shaped" greater sciatic notch, smaller and differently oriented iliac auricular region, relatively large proximal and distal femoral ends, very large acetabulum, truncated calcaneus (Rak 1990; Sawyer and Maley 2005; Trinkaus 1983; Trinkaus and Howells 1979)], they conform to the basic configurations summarized above, including a femoral "carrying angle" and a lumbar curve. Known Middle Pleistocene pelvic remains from Sima de los Huesos (Arsuaga et al. 1997), Arago (Day 1982) (personal observation), and Jinniushan (Rosenberg and Lu 1997) differ from *Homo sapiens* in some iliac details (e.g., flare, anterior superior iliac spine) but can otherwise be accommodated by Pilbeam's pelvic criteria. The Sima de los Huesos femora also present a carrying angle (Day 1986).

According to Rose (1984), os coxae KNM-ER 1808, KNM-ER 3228, and OH 28 are generally similar to *Homo sapiens* and *H. neanderthalensis* but differ in having relatively larger anterior iliac regions. Scrutiny of OH 28 (cast) reveals,

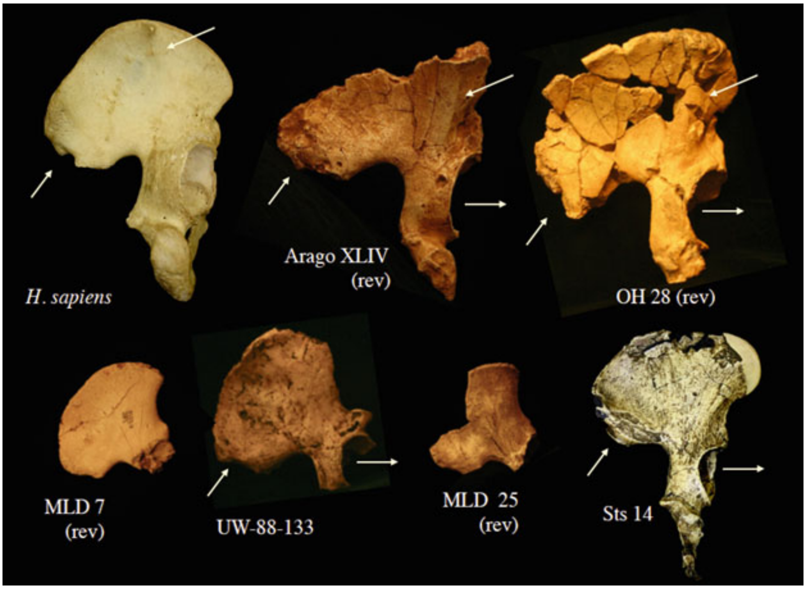

Fig. 1 Os coxae of *Homo sapiens* and various hominids with the ilium oriented laterally. Note differences in development of iliac pillar in *H. sapiens*, Arago XLIV, and OH 28, and virtual nondevelopment in "australopiths." Also note differences in anterior and posterior iliac expression and especially in orientation of the acetabulum, which, if in the anatomical position, would reposition the ilium of all but *H. sapiens* posteriorly. See text for further discussion; not to scale; *rev* reversed (All specimens except *H. sapiens* and Sts 14 courtesy of the American Museum of Natural History)

however, that this specimen contrasts with *H. sapiens* as *H. neanderthalensis* does, e.g., in asymmetry of anterior versus posterior iliac proportions and curvature, thickness and anterior position of the external iliac pillar, thickness of the ilium posteriorly, and small size of the auricular surface (personal observation) (Fig. 1). Further, although Day (1986) claimed morphological similarity between OH 28 and Arago XLIV, the latter clearly differs not only in the massiveness of its ilium but in details such as a sigmoidally symmetrical and shallow anteroposterior iliac crest curvature, deep and uniform greater sciatic notch angle, large auricular surface, and huge acetabulum (personal observation) (Fig. 1). These inconsistencies raise questions not only about the suggested similarities between the pairs previously compared OH 28-Arago XLIV, KNM-ER 1808–3229, and Nariokotome KNM-WT 15000-Gona BSN49/P27 partial os coxae, but also about similarities claimed to exist among them all (Day 1986; Simpson et al. 2008; Walker and Leakey 1993).

A preliminary reassessment of the comparability of these OH, Arago, KNM, and BSN pelvic specimens based on casts and published images proves potentially interesting. For example, when orienting the acetabula in anatomical position, the "inner" iliac blade surfaces of all specimens face forward/anteriorly, as they do in Sts 14 and Al 288-1, and not medially, as in *H. sapiens*, *H. neanderthalensis*, and SK 50. Further, reconstructions of KNM-WT 15000 (e.g., as in the Neanderthal Museum)

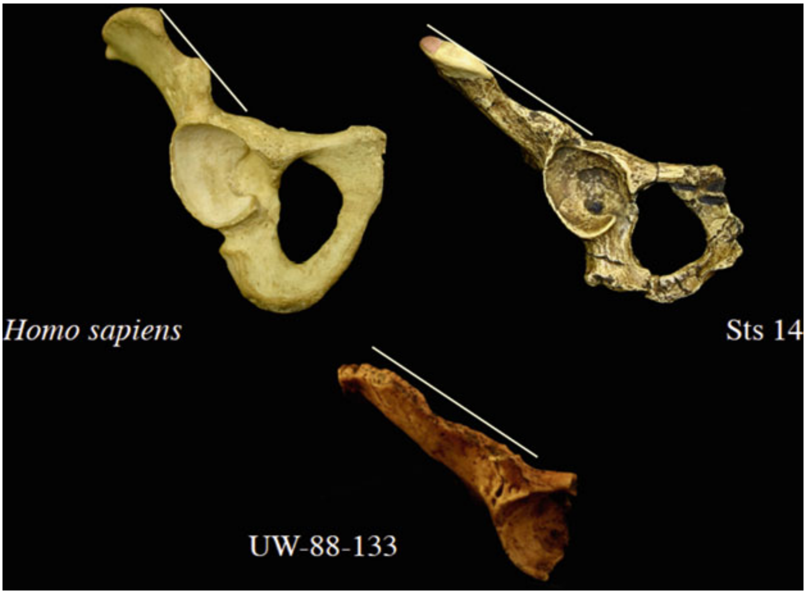

Fig. 2 Right os coxae of *Homo sapiens*, Sts 4, and Malapa MH1 (UW-88-133) to illustrate, e.g., differences between the former and the latter two in details of the pubic and ischial regions and especially iliac superoinferior height and lateral flare. See text for further discussion; not to scale; reproduced to same size (Cast of UW-88-133 courtesy of the American Museum of Natural History)

and the Gona pelvis, BSN49/P27 (Simpson et al. 2008), portray the respective ilia tilting laterally outward with their “inner” surfaces turning somewhat upward, albeit not as markedly as in some australopiths (see below, e.g., Sts 14, Al 288-1).

Sts 14’s superoinferiorly low and squat, posteriorly rounded and expanded, and clearly anteroposteriorly long ilia incorporate a well-defined greater sciatic notch (Figs. 1 and 2). In these features, the small Hadar AL 288-1 left os coxa, juvenile Makapansgat ilia MLD 7 and 25, Malapa UW-88-133, the virtually reconstructed *Ardipithecus* ARA-VP-6/500, and apparently the Swartkrans right partial os coxa SK 50 are similar to Sts 14 (Kibii et al. 2011; Lovejoy et al. 2009b) (see Figs. 1 and 2). Adult ilia Sts 14, AL 288-1, and likely also SK 50 differ from earlier-discussed specimens in being oriented more laterally outward than vertically, with concomitantly greater superior exposure of the internal iliac surface and more subdued “S”-shaped iliac crests; further, these specimens bear only moderately thickened iliac (crest) tubercular regions and poorly developed iliac pillars (Day 1986; Johanson et al. 1982; Robinson 1972). The virtual reconstruction of *Ardipithecus* portrays a more vertically and anteriorly oriented ilium, more open and poorly delineated greater sciatic notch (especially regarding defined posterior superior and inferior iliac spines), and a longer pubic ramus than the virtual reconstruction of Al 288-1 (Lovejoy et al. 2009b).

Australopith anterior ilia present a dichotomy of morphology. In the better-preserved left os coxa of Sts 14, this region appears to be roundedly expanded anteriorly (Robinson 1972), as in StW 431 (Toussaint et al. 2003) and AL 288-1 (Johanson et al. 1982). Thus, a definitive anterior superior iliac spine cannot be identified. But in SK 50, even though its iliac crest is damaged along much of its length, what is preserved continues forward to become a well-defined, beak-shaped anterior superior iliac spine that projects markedly anterior to a bluntly thickened, almost knoblike anterior inferior iliac spine (Day 1986; Robinson 1972). The smaller Makapansgat juvenile ilia (MLD 7 and 25) are similar to SK 50 (but not to Sts 14 and AL 288-1) in having a projecting, beaklike anterior superior iliac spine (Dart 1957). Although differing from SK 50 and MLD 7 and 25 in the region of the anterior superior iliac spine, Sts 14 and AL 288-1 are similar to them in developing a knoblike anterior inferior iliac spine that lies noticeably superior to and back over the superior margin of the acetabulum, as in other potential hominids surveyed above.

Although australopiths have traditionally been interpreted as postcranially intermediate between knuckle-walking great apes and *Homo* – as noted, for instance, in their developing a humanlike posterior iliac expansion while supposedly retaining an apelike anterior iliac distension – this scenario seems inappropriate: not all specimens present similarly configured anterior superior iliac spines. Indeed, only SK 50 and MLD 7 and 25 compare favorably with great apes in having a beaklike anterior superior iliac spine that continues forward the trajectory of the iliac crest. The rounded anterior expansion of this region in Sts 14, AL 288-1, and apparently also in Malapa UW-88-133, while absolutely and relatively large compared to *Homo sapiens* and other possible fossil hominids, is, nevertheless, derived in its own right.

The preserved pubic rami of Sts 14 and AL 288-1 are reminiscent of this region in Neanderthals and the Jinniushan specimen in being relatively long, but the symphyseal regions of the australopith specimens are not also superoinferiorly tall and anteroposteriorly compressed (Rosenberg 1998). A superior view of the articulated Sts 14 pelvis illustrates (in contrast to *Homo sapiens*) the relation of the elongate pubic rami to the relatively wide pelvic canal and the relatively posterior positioning of the outwardly flared ilia (Robinson 1972). Further, while in *H. sapiens* (and other Pleistocene specimens surveyed above) the curve of the iliac crest positions the anterior superior iliac spine just lateral to the parasagittal plane intersecting the posterior superior iliac spine, in Sts 14, the anterior portion of the ilium would have been situated well lateral to the plane of the sacroiliac articulation (Robinson 1972). The known left os coxa of AL 288-1 was likely similar to Sts 14 (Johanson et al. 1982). Although SK 80's iliac crest is similar to Sts 14 in not being strongly "S shaped," when their iliac blades are oriented in the same plane, SK 80's acetabulum is similar to *H. sapiens* in facing laterally and slightly downward (Robinson 1972). In contrast, the fairly vertically aligned Sts 14 acetabulum faces forward. When compared in anatomical position, the Sts 14 ilium is again more outwardly and obliquely oriented, while SK 50 is more anteroposteriorly arranged, as in *H. sapiens* and various other specimens attributed to *Homo*.

Although Malapa MH1 and MH2 are presented as having medially facing and vertically oriented ilia (Kibii et al. 2011), the largely complete right *Australopithecus sediba* ilium UW-88-133 (cast) can reasonably be oriented with more outward lateral flare (Figs. 1 and 2). This also appears to be the case with the reconstructed os coxa of *Ardipithecus ramidus* ARA-VP-6/500 (Lovejoy et al. 2009b) (see below).

Another feature of potential phylogenetic significance is the distance between the ischial tuberosity and the inferior acetabular lip, which is quite pronounced in great apes and apparently in catarrhines in general (Aiello and Dean 1999). The separation is marked in SK 50, shorter in Sts 14 and KNM-WT 15000, and minimal in *Homo sapiens*, in which a deep groove intervenes between the two structures. Perhaps further study of this region will prove enlightening, if not in defining features of clade Hominidae, perhaps in delineating a subclade/s within Hominidae.

Unfortunately, many details of the vertebral column in general are unknown. Of particular note is that while the lumbar region of KNM-WT 15000 is somewhat curved and angled inward at L5-S1, unlike *H. sapiens, H. neanderthalensis*, and large-bodied apes, this individual had six rather than five lumbar vertebrae (Walker and Leakey 1993).

Regarding femora, KNM-WT 15000, KNM-ER 1481 and 1472, Sts 34A, AL 129-1a, and UW 88-63 (casts) and D4167 (original) present carrying angles that set them apart from Sts 34B, AL 333-4, Trinil 3/Pith I, and Spy 1 (Table 1; see also Fig. 3) (Lordkipanidze et al. 2007; Walker and Leakey 1993). For the former seven specimens, medial distal femoral angles range between 103° and 110° and lateral angles between 70° and 77°; using Martin's bicondylar angle [measured between the axis perpendicular to the distal articular plane and the lateral angle (Martin 1928)], the range of this sample is 13–20°. In contrast, distal femoral angles of the Sts 34B et al. specimens are lower, i.e., below 103° (medial), 77° (lateral), and 13° (Martin's scale). Further, Sts 34A and Sts 34B also differ in size and detail of condylar shape and orientation (Table 1). As tabulated by Tardieu and Trinkaus (Tardieu and Trinkaus 1994), bicondylar angles for several living human populations (males and females pooled) range between 8.5° and 10.5° (Martin's scale). The fact that two "groups" are distinguishable on the basis of distal femoral angle – with *Homo sapiens* falling into, or at least not with, one of them – raises doubt about the allocation to genus *Homo* of specimens preserving the distal femur (especially KNM-WT 15000, KNM-ER 1481 and 1472, and D4167) as well as specimens presenting pelvic as well as vertebral and other features not covered here that have been deemed australopith-like. Indeed, as will become clearer below, these inconsistencies redound, in broad perspective, on defining genus *Homo* on the basis of *sapiens*-like "striding bipedalism" (Wood and Collard 1999) (see also chapter "▶ Defining the Genus *Homo*," Vol. 3) and, more specifically, on assuming because of similar age and/or location, that specimens (e.g., those from Dmanisi) must represent not only the same taxon but a paleodeme of it that morphological difference represents not taxi diversity but merely individual variation (Lordkipanidze et al. 2013; Margvelashvili et al. 2013). In the case of the Dmanisi specimens, if, as the skulls and mandibles have been designated, D4167 represents *H. erectus*, then, at least with regard to distal femoral angle, there is no basis for taxonomically discriminating between any of the specimens discussed here where similar distinctions are demonstrable (see below).

Table 1 Distal femur: carrying angle and morphology

Specimen	Medial condyle angle (°)	Lateral condyle angle (°)	Martin's bicondylar angle (°)	Published bicondylar angle (°)[a]	Medial vs. lateral condyle height	Patellar facet	Popliteal fossa	Inferior profile	Medial vs. lateral condyle configuration
Extant humans				10.5–8.5 (sexes pooled)	Shorter anteriorly	Asymmetric, narrow	Narrow "V"	Tall, narrow trapezoid	
AL 129-1a	110	70	20	13	Shorter anteriorly	Asymmetric, wide	Wide	Very wide rectangle	Both curve, parallel
KNM-WT 15000	108	72	18	18	Equal height	Symmetric, wide	Moderately wide	Moderately wide trapezoid	Both straight, diverge
D4167	105	75	15		Much taller anteriorly	Asymmetric, wide	Moderately wide	Wide, odd trapezoid	Both curve
Sts 34A	105	75	15	15	Shorter anteriorly	Asymmetric, narrow	Narrow "V"	Rounded, wide, semi-trapezoid	Medial A/P deeper, both curved
AL 333w-56	105	75	15		Taller anteriorly	Asymmetric, wide, shallow	Narrow, widens?	Wide, rectangle	Slight arc, parallel
KNM-ER 1481	104	76	14	10	Much shorter anteriorly	Asymmetric, moderately wide	Wide, deep	Moderately tall, odd trapezoid	Medial angle > lateral
Sts 34B	103	77	13		Equal	Symmetric, wide, deep	Widens posteriorly	Wide, short-angle triangle	Medial teardrop, lateral straight
KNM-ER 1472	103	77	13	13	Taller anteriorly	Asymmetric, moderately wide	Moderately wide, deep	Wide trapezoid	Medial curve > lateral

(*continued*)

Table 1 (continued)

Specimen	Medial condyle angle (°)	Lateral condyle angle (°)	Martin's bicondylar angle (°)	Published bicondylar angle (°)[a]	Medial vs. lateral condyle height	Patellar facet	Popliteal fossa	Inferior profile	Medial vs. lateral condyle configuration
UW-88-63	103	77	13		Much shorter anteriorly	Asymmetric, wide	Moderately deep, wide	Wide, moderate trapezoid	Medial curve, lateral straighter
TM 1513	103	77	13		Shorter anteriorly	Asymmetric, narrow	Narrow	Tall, narrow trapezoid	Medial curve, lateral straighter
LB1	102	78	12		n.a.	n.a.	n.a.	n.a.	n.a.
Spy 1	98	82	8	9	Much shorter anteriorly	Asymmetric, narrow, deep	Deep, moderate	Moderately wide trapezoid	Medial slight curve, lateral straight
AL 333-4	98	82	8	9	Equal height	Symmetric wide, shallow	Wide, deep	Very wide rectangle	Medial curve, lateral straighter
Trinil 3/Pith I	97	83	7		Shorter anteriorly	Asymmetric, wide	Narrow, deep	Moderate trapezoid	Medial curve, lateral straighter

[a] See Table 2 in Tardieu and Trinkaus (1994)

Fig. 3 Femora of *Homo sapiens*, TM 1513, Dmanisi D4167, KNM-WT 15000, and Sts 34B illustrating similarities in all but *H. sapiens* distally in bicondylar/carrying angle and proximally in lack of a distinct intertrochanteric line and posterior orientation of the lesser trochanter. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

As Robinson (1972) long ago recognized, the distal femur presents much morphology of potential significance (see Fig. 4). For instance, as he saw it, when viewed from below, distal femora TM 1513 (left) and Sts 34 (right distal femur, now identified as Sts 34B) are generally similar to those of large-bodied apes in disparity and/or orientation of medial versus lateral condyle but differ in being deeper anteroposteriorly and more trapezoidal (mediolaterally narrower anteriorly) rather than rectangular in outline and in having a somewhat more concave and slightly asymmetrical patellar fossae, in concert with the lateral margin being more anteriorly distended than the medial margin (in other words, when viewed from below, the lateral condyle is anteroposteriorly longer than the medial, regardless of differences in configuration). Robinson's enthusiasm notwithstanding, study of casts of these specimens reveals that while TM 1513 displays (slight) patellar fossa and condyle asymmetry, Sts 34B's fossa is symmetrical and its condyles equally distended anteriorly (Table 1). Also, the curvature of the medial condyle is much more severe in TM 1513 than in Sts 34B, in which (uniquely for hominids studied here) it is "teardrop" shaped (Table 1). Interestingly, Sts 34B also differs markedly from Sts 34A in overall and specific distal femoral features – which is consistent with the craniodental nonuniformity of Sterkfontein fossils (Schwartz and Tattersall 2005).

Distal femora AL 129-1a and AL 333-4, of which the latter is the larger (McHenry 1986), also differ in morphological detail (Table 1). Lague (2002) acknowledges size and some morphological difference between the two

Fig. 4 Distal views of right femora of *Pan troglodytes* (=*Pan trog.*), Sterkfontein TM 1513, *Homo sapiens*, AL 333–4, KNM-ER 1472, AL 288-1a, and UW 88–63 (Malapa hominid 1) and left femora of KNM-ER 1482 and KNM-WT 15000. Note differences in, e.g., anteroposterior length, orientation and relative sizes of medial and lateral condyles, and relative depth and symmetry versus asymmetry of the patellar surface. Also note specific differences between AL 333–4 and AL 129-1a in, e.g., anteroposterior length, crispness of lateral patellar surface border, lateral epicondylar morphology, and divergence posteriorly of medial and lateral condyles; although AL 129-1a is damaged anteromedially, it is likely that this region would not have projected as far anteriorly as in AL 333–4. Of further note is that UW 88–63 resembles only KNM-ER 1481 and only in degree of asymmetry of the region of the patellar surface. See text for detailed discussion; not to scale; images reproduced to similar mediolateral width; *r* reversed (Except for TM 1513, all casts courtesy of the American Museum of Natural History)

specimens – especially the anterior projection of the medial margin of the patella fossa – but claims this merely reflects sexual dimorphic variation typical of extant populations of large-bodied hominoid species. If true, then a number of fossils that differ in ways similar to AL 129-1a and AL 333-4, or in other morphologies (Table 1), should be regarded as variants of the same subspecies. I am not suggesting that one ignore intraspecific variation, which includes sexually dimorphic differences. However, one can only address this topic after hypothesizing "groups" (e.g., morphs at least) within the morphological parameters of which individual variation can be assessed (Schwartz 2007b). Further, by focusing on general shape and outline, Lague overlooks differences between AL 129-1a and AL 333-4 not only in carrying/bicondylar angle but also in morphological detail (Table 1), beyond which are yet-to-be studied distinctions in, e.g., condylar side, epicondylar, epicondylar line, popliteal surface, and diaphyseal cross-section configurations (personal observations). Indeed, it appears that at present geometric-morphometric analyses are not capable of capturing the morphological details required of systematic analyses (e.g., see Lordkipanidze et al. 2013; see also Ulhaas 2007).

Turning to the proximal femur (Table 2), the most commonly reported "feature" is the femoral neck-shaft angle (measured inferiorly/medially at the intersection of the long central axes of the neck and shaft). As implied by DeSilva et al. (2013), Neanderthals display a moderate amount of variation and *Homo sapiens* considerable variation, the range of the latter encompassing virtually all other hominids. Gilligan et al. (2013) have argued that differences among *sapiens* populations in femoral neck-shaft angle are strongly correlated with differences in climate as well as in aspects of lifestyle, including types and use of clothing. Although neither the ontogeny of this angle nor its relation to the carrying/bicondylar angle has been studied, Gilligan et al.'s conclusion, at least with regard to the influence of lifestyle and clothing, is intriguing. For, if even partially correct, it suggests that the variability recorded for *sapiens*, and likely also for *neanderthalensis*, does not negatively impact the potential phylogenetic significance of the proximal femoral morphology of hominid species that were not geographically widespread and thus subject to disparate climates. Geographic and climatic restrictiveness also suggests that at least femoral neck-shaft angle differences are not due to climate-related clothing, if consideration of clothing of any sort is actually relevant. In other words, morphological variability in the species *Homo sapiens*, as well as in the species *H. neanderthalensis*, does not necessarily lead to the conclusion that variability is the sole explanation for difference among hominid specimens. Thus, while White (2003, 2012) remains steadfastly and zealously critical of paleoanthropologists who are "biased" toward identifying taxic diversity in the human fossil record, he is not exempt from bias toward explaining virtually all morphological difference as variation. Both claims should be regarded as hypotheses in need of testing (see also chapter "▶ General Principles of Evolutionary Morphology," Vol. 1).

Returning to the femoral neck-shaft angle, it is potentially noteworthy that non-*sapiens*/*neanderthalensis* specimens commonly regarded as *Homo* do not cluster together (Table 2). Rather, in this sample, the angle in the majority of specimens is 120°, in two it is 125°, and in most others it is 130°. Further, no "group," even excluding those with 125° angles, conforms to any traditionally recognized hominid taxon or clade. Interestingly, Dmanisi D4167 has the lowest angle: 113°. The paucity of complete femora limits comparisons involving femoral shaft-neck and carrying/bicondylar angles, which, as seen, for instance, in D4167 (113°/15°), KNM-WT 15000 (120°/18°), KNM-ER 1472 (120°/13°), and Trinil 3/Pith I (120°/7°) (Tables 1 and 2) would appear informative for both systematic and locomotory deliberations.

Elsewhere, I (Schwartz 2007a) suggested that the posterior position/orientation of the lesser trochanter in South and East African "australopiths" and also KNM-WT 15000 (posterior) distinguished them not only from mammals in general but also from *Homo sapiens*, *H. neanderthalensis*, and from *Orrorin*, in which this structure points medially and is therefore visible when the femur is viewed anteriorly (Figs. 5, 6, and 7). Additional scrutiny of specimens (actual and casts) as well as review of the literature not only substantiates this observation but also

Table 2 Proximal femur: neck/shaft angle and morphology

Specimen	Neck angle (°)	Relative neck length	Neck profile (anterior)	Relative head size	Head extension distal	Head extension proximal	Lesser trochanter position	Lesser trochanter shape	Greater trochanter height	Intertrochanter crest	Spiral line	Gluteal line
STW 25	n.a.	n.a.	Likely tapered	Small	No	No	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
STW 30A	n.a.	n.a.	Taper	Small	Yes	No	n.a.	n.a.	n.a.	n.a.		
STW 30B	n.a.	n.a.	Taper	Small	Yes	No	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
UW 88-89	n.a.	n.a.	n.a.	Small	Some	Some	Medio-posterior	Slight pointy	n.a.	n.a.	n.a.	n.a.
OH 28	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Posterior	n.a.	n.a.	n.a.	Faint	Stouter
ARA-VP-1/701	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	Fairly medial	Large blunt	n.a.	n.a.		
H. sapiens	111–140	Short	Parallel	Large	Yes	Yes	Very medial	Large blunt	Well above	Distinct	Marked	Marked
H. neanderthalensis	113–127	Short	Parallel	Large	Yes	Yes	Medial	Large blunt	Above	Distinct	Marked	Marked
D4167	113	Long	Slight taper	Moderately large	Yes	Yes	Medio-posterior	Blunt	Above	Moderate	Marked	Marked
UW 88-04/05/39	120	Long	Slight taper	Medium?	Yes	No	Very posterior	Large	n.a.	Faint		
OH 20	120	Long	Taper	n.a.	n.a.	Likely	Posteromedial	Likely pointy	No	Faint	Marked	Faint
BAR 1002’00	120	Moderately long	Slight taper	Moderately large	Yes	Yes	Fairly medial	Long	Likely above	Faint	Faint	Faint
KNM-WT 15000 (R)	120	Long	Some taper	Medium	Slight	Slight	Very posterior	Slight point	n.a.	n.a.	None	Faint

SK 97	120	Long	Taper	Medium	Yes	Some	Posteromedial	Pointy	Slight	Distinct	Visible	Faint/ damaged
MAK VP1/1	120	Long	Taper	Likely small	No	No	Posteromedial	Blunt	Well above	Faint	Absent	Faint
AL 333-3	120	Moderate	Some taper	Large	Yes	Yes	Posteromedial	Long?	Some	Faint	n.a.	n.a.
KNM-ER 1472	120	Moderate	Some taper	Large	Yes	Yes	Medio-posterior	Pointy	Noted	Moderate		
KNM-ER 1481	120	Moderate	Some taper	Large	Yes	Yes	Posteromedial	Blunt	Noted	Moderate	Faint	Faint
Trinil 3/Pith I	120	Short	Parallel	Large	Some	Some	Medial	Pointy	Noted	Distinct	Marked	Marked
KNM-ER 815	125	Very long	Some taper	Probably small	Slight?	None?	Posteromedial	Pointy	n.a.	Faint	Faint	Blunt
KNM-WT 15000 (L)	125	Long	Some taper	Medium	Slight	Slight	Very posterior	Slight point	Slight	Faint	Faint	Faint
Trinil 6/Pith II	130	Long	Some taper?	Small–medium?	n.a.	n.a.	Medio-posterior	Not long	n.a.	None?	Faint	Faint
AL 288-1	130	Long	Some taper	Small	Yes	Yes	Posteromedial	Pointy	Noted	Faint	Very medial	Very lateral
KNM-ER 999	130	Very long	n.a.	Probably small	Likely yes	Likely yes	Posteromedial	Pointy	n.a.	Faint	Faint	Faint
AL 128-1	130	n.a.	Taper	n.a.	n.a.	n.a.	Posteromedial	Long	Slight	Faint	Marked	Faint
KNM-ER 738	130	Very long	Some taper	Moderate	Noted	Some	Posterior	Pointy	Some?	Faint	Moderate	Faint
OH 62	130	Long	Some taper	Likely small	No	No	Very posterior	Long	n.a.	n.a.		
LB1	130	Moderate	Slight taper	Large	Yes	Yes	Medial	Blunt	Above	Distinct		

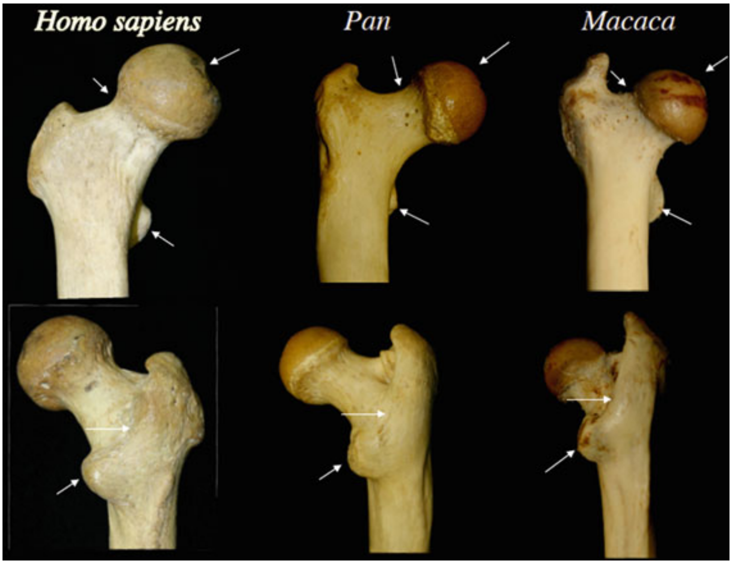

Fig. 5 Right proximal femora of *Homo sapiens*, *Pan*, and *Macaca* (*top row*, anterior; *bottom row*, posterior) illustrating typical primate/mammalian features, e.g., short neck, large rounded head, medially projecting lesser trochanter, and stout intertrochanteric line (*arrows*). See text for further discussion; not to scale (Copyright © J. H. Schwartz)

demonstrates that, like KNM-WT 15000, many specimens allocated to *Homo*, including D4167 (Lordkipanidze et al. 2007), are "australopith"-like in having a somewhat-to-extremely posteriorly oriented lesser trochanter (Table 2; Fig. 6). These specimens are also "australopith"-like in presenting, for example, a relatively long, medially tapering, and somewhat anteroposteriorly compressed femoral neck; relatively small-to-moderate femoral head with little or no distension beyond the perimeter of the neck, especially proximally; and a weakly developed intertrochanteric line (see Table 2 for additional features).

Since, as previously pointed out (Schwartz 2007a), some features seen in *H. sapiens* are typical of mammals, and essentially of all primates (e.g., Fig. 5), those that differ – as in "australopiths" and "australopith-like *Homo*" – are plausibly interpreted as derived or clade informative. In other words, such non-*sapiens* features would unite a group that consists of various specimens ascribed to *Homo*, to the exclusion of *H. sapiens* and *sapiens*-like hominids including, given preserved femoral morphology, *Orrorin* and *Ardipithecus* (see Tables 1 and 2). Consequently, because in the broad comparison "australopith"-like features emerge as derived relative to *sapiens*-like features, no "australopith"-like taxon (e.g., *Australopithecus sediba* represented by Malapa UW-88-04/05/39) should be considered "ancestral" to any specimens, and consequently taxa, that may constitute a *Homo* clade.

Further, as noted previously (Bartsiokas and Day 1993; Day 1973; Kennedy 1983), Trinil 3/Pith I (complete) and Trinil 6/Pith II (partial proximal) femora are

Fig. 6 Proximal femora of various hominids: Dmanisi D4167 and casts of KNM-WT 15000, SK 97, and KNM-738 (*top row*, anterior; *bottom row*, posterior) illustrating atypical primate/mammalian features, e.g., long neck, small head, posteriorly projecting lesser trochanter (*arrows*), and weak intertrochanteric, spiral, and/or gluteal lines. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

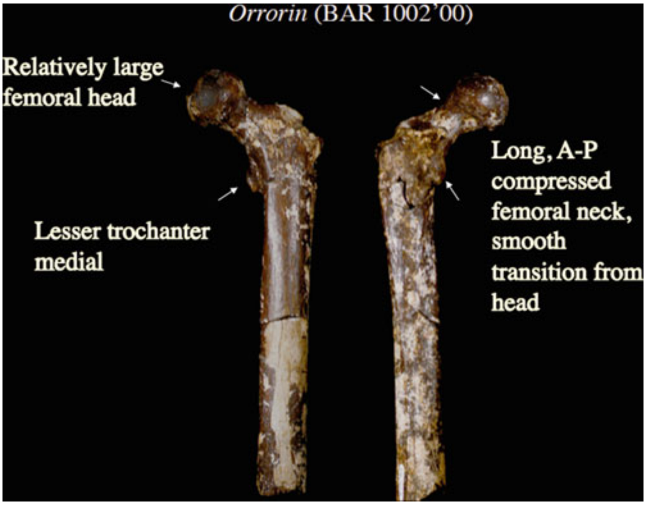

Fig. 7 Left proximal femur of *Orrorin* (*left*, anterior; *right*, posterior views). See text for further discussion; not to scale (Copyright © J. H. Schwartz)

morphologically dissimilar. More specifically, the former specimen presents *sapiens*- and the latter "australopith"-like features (Table 2). However, contrary to suggestions that all non-Trinil 3 (complete) femora constitute a group (Bartsiokas and Day 1993; Day 1973; Kennedy 1983), Trinil 3/Pith I (complete), Trinil 3/Pith III (shaft), and Trinil 9/Pith IX (shaft) are distinguished in diaphyseal shape and proximal morphological detail from Trinil 6/Pith III, and Trinil 8/Pith IV (shaft), which resemble each other morphologically (personal observations).

Regarding pedal morphology, foot bones attributed to *Ardipithecus ramidus* (Lovejoy et al. 2009c) and a specimen described as *Ardipithecus*-like (Haile-Selassie et al. 2012) lacked an arch, had fully opposable halluces, and did not "toe off" with this digit. Day and Napier (1964a, b) reconstructed the OH 8 foot bones with an arch and a first digit in alignment with the other digits; but restudy suggests that the hallux was probably semi-opposable and, by extension, there was an absence of an arch (Clarke and Tobias 1995). The latter two features characterized StW 573 ("Little Foot") (Clarke and Tobias 1995). In contrast, tarsals attributed to *Australopithecus afarensis* (Latimer and Lovejoy 1990; Ward et al. 2011) and *Au. sediba* (DeSilva et al. 2013; Zipfel et al. 2011) are interpreted as presenting an arch, with other preserved pedal elements of *Au. afarensis* indicating a fully adducted hallux. Clearly, Pilbeam's pedal features do not define a hominid clade.

To review, some features of the os coxa and femur, in contrast to at least other catarrhines, appear to distinguish a hominoid clade that we could call "hominid," i.e., a long pubic ramus, a superoinferiorly short ilium that is roundedly expanded posteriorly, some thickening in the region of an iliac (crest) tubercle, a well-developed and knoblike anterior inferior iliac spine that lies noticeably superior to and somewhat back over the superior acetabular rim, a deep greater sciatic notch, a defined linea aspera, development of an obliquely oriented femoral shaft (producing a carrying/bicondylar angle), and a concave lateral tibial facet for the femur that is at the same level as the (also but primitively concave) medial facet, with the two facets being separated by well-developed tubercles. Within this potential clade, a subclade appears to be distinguishable even just on features of the proximal femur – e.g., long neck, posteriorly directed lesser trochanter, poorly delineated head/neck cervical region, and weakly defined intertrochanteric line – and another, which may be a subclade of the latter, in presenting a medially tapering neck.

More Recently Suggested Postcranial Features of "Erect Posture"

With the discovery at Kanapoi and Allia Bay, Kenya of specimens attributed to the species *Australopithecus anamensis*, Leakey et al. (1995) presented features of the proximal tibia (via right proximal tibia KNM-KP 29285A) they thought distinguished hominids from apes and, by extension, from other catarrhines. For example, in apes, the medial tibial condylar facet is convex and in posterior view situated slightly higher than the gently concave lateral condylar facet and, in frontal view, the shaft does not flare out smoothly and evenly to the margins of the proximal articular surface (i.e., the proximal articular surface extends especially medially and laterally farther than

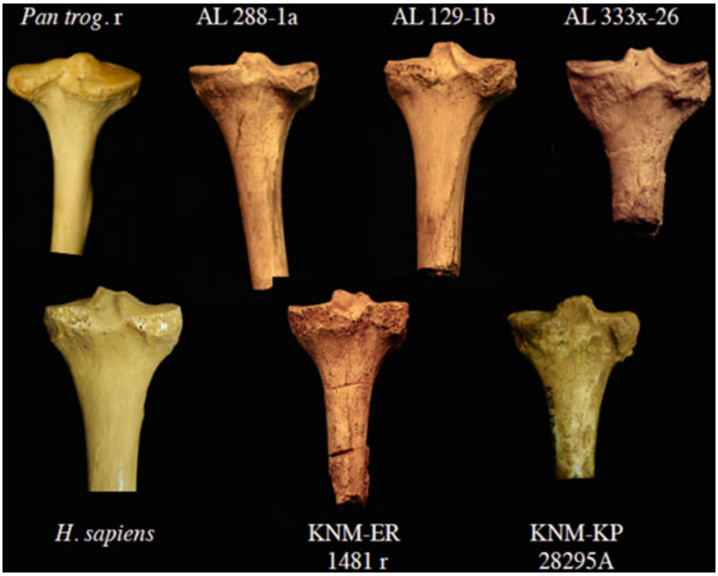

Fig. 8 Posterior views of right proximal tibiae of *Homo sapiens*, AL 288-1a, AL 129-1a, AL 333x-26, and KNM-KP 28295A and left proximal tibiae of *Pan troglodytes* (=*Pan trog.*) and KNM-ER 1481. See text for further discussion; not to scale; *r* reversed (Casts of AL 288-1a, AL 129-1a, AL 33x-26, and KNM-ER 1481 courtesy of the American Museum of Natural History)

the respective margins of the shaft). Further in apes, the two condylar facets are separated by a single, blunt tubercle [see also Aiello and Dean (1999)]. In contrast, Leakey et al. suggested, in specimens attributed to "accepted" australopith taxa as well to species of *Homo*, both tibial condylar facets are at least somewhat concave, separated by a pair of well-defined tubercles and, in posterior view, level with one another. Further in hominids, in anterior view, the tibial shaft flares out to meet the medial and lateral margins of the proximal articular surface. Although these distinctions apply in general to apes and extant humans (in which the tubercles are actually variably distinct), they do not completely describe "australopiths" (Fig. 8).

For example, in right proximal tibia AL 288-1a (cast), the lateral condylar facet is slightly convex while the medial is slightly concave; viewed from behind, medial facet lies slightly below the level of the lateral facet (Fig. 8). Further, the apically indistinct tibial tubercles are separated by and incorporated into a mediolaterally wide blunt, loph-like structure that is anteroposteriorly obliquely oriented from the medial to the lateral side. Right proximal tibia AL 129-1b (cast) is similar to Al 288-1a in overall size, concaveness versus convexity and disparity in height of the condylar facets, and in having indistinct tubercles incorporated into a loph-like structure but differs in the shapes of the facets, a more posterior placement of a taller intertubercular loph, and in a different orientation of the shaft. In the large right proximal tibia AL 333x-26 (cast), the cuplike condylar facets are markedly concave (more so than any other suspected hominid) and, as seen from behind, lie at the same level; also the tibial tubercles are symmetrically distinct at their tips and incorporated into a tall loph that is mediolaterally oriented and situated farther posteriorly. As seen in a cast of the large right proximal tibia KNM-KP 29285A, which is part of the published hypodigm of *Australopithecus anamensis* (Leakey et al. 1995), the lateral condylar facet is faintly while the medial facet is a bit more obviously concave; the two facets are separated by indistinct tubercles that present themselves as a single blunt, high-rising structure that is posteriorly situated on the proximal surface. From behind, the posteriorly sloping lateral condylar facet lies slightly higher than the medial facet. Finally, in left proximal tibia KNM-ER 1481 (cast), both condylar facets are somewhat concave; when viewed from behind, the medial facet lies slightly above the level of the lateral facet. In all of these tibial specimens, KNM-KP 29285A included, the medial margin of the shaft flares out toward the proximal articular region below which the profile actually swells (either slightly as in KNM-KP 292895A, AL 288-1am AL 129-1b, and *H. sapiens* or noticeably as KNM-ER 1481 and AL 333x-26). Also in these specimens, with the notable exception of *H. sapiens*, the lateral border of the shaft flares out slightly before terminating below the proximodistally relatively tall, somewhat squared-off overhang of the lateral portion of the proximal articular region with which the fibula articulates (Fig. 8). Interesting, in *H. sapiens*, the medial and lateral borders of the shaft fan out more or less symmetrically as they approach the proximal end with greater swelling occurring on the lateral rather than the medial side.

As is evident even from this small tibial sample, the possession of a concave lateral femoral condylar facet that lies level with the medial facet, a pair of apically distinct tubercles, and a more symmetrically flared proximal shaft does not fully characterize *Homo sapiens* (and *H. neanderthalensis*), and they certainly do not a hominid make. Indeed, the only tibial feature Leakey et al. (1995) discussed that could distinguish a hominid from an ape is the flaring and swelling of the medial profile of the shaft as it converges upon the proximal articular region – which, in its more swollen state would represent a more derived configuration. Features of the proximal tibia not detailed here (e.g., symmetry/asymmetry of condylar facet shape, orientation of condylar facets, configurations of intercondylar facet depressions, height of tubercular region) are also consistent with the picture of nonuniformity not only among this sample of "australopiths" but also among specimens from Hadar, among which the distinctiveness of AL 333x-26 alone makes clear that "australopith" systematics is far from being resolved (for another perspective, see chapter "▶ The Species and Diversity of Australopiths," Vol. 3). Further, proximal tibial as well as femoral morphology (see above) confirms observations based on dental morphology (Schwartz and Tattersall 2005), namely, that the Hadar specimens encompass more than one taxon. At a higher taxonomic level, since various "australopiths" retain primitive tibial features – e.g., convex medial condylar facet, medial facet higher than lateral facet, indistinct tibial tubercles, and asymmetrically flared proximal shaft – features Leakey et al. put forward as defining hominids appear instead to unite a subclade or subclades within it.

Since tibial and femoral morphologies reflect aspects of locomotion, the differences noted here between specimens suggests, as pedal morphology has begun to indicate, that "bipedalism" was enacted differently among different species or subclades of hominid (see also chapter "▶ Origin of Bipedal Locomotion," Vol. 3). Since no Hadar specimen is dentally comparable to the type specimen of *Au. afarensis*, Laetoli hominid (LH) 4, and all Laetoli specimens can reasonably be allocated to the same dental morph (Schwartz and Tattersall 2005), it would be interesting to know the postcranial morphology of the hominid – that is, of *Au. afarensis* – that left the footprints. Further, the singular degree to which the tibial condylar facets of AL 333x-26 are depressed and cuplike not only reflects a uniquely derived configuration but also likely a unique type of hominid locomotion.

In their description of the Lukeino proximal femur (BAR 1002'00), Pickford et al. (2002) commented on how slight the linea aspera is compared to specimens of australopiths and *Homo* (because the spiral line of BAR 1002'00 does not meet the gluteal/3rd trochanteric line to form a linea aspera of high relief). I agree with this general description (personal observation; Fig. 7). They (p. 202) then suggested, because apes do not present a muscle scar descending from the region of the gluteal tuberosity, that such "a precursor of the *linea aspera*" is a hominid-identifying feature related to bipedalism. A review of casts of some femora identified as australopith or *Homo* reveals, however, a more complex picture (Table 2). For instance, KNM-WT 15000, the supposedly first humanlike striding biped, lacks a spiral line altogether. Other specimens differ in presence and degree of expression of a gluteal line (Table 2), as well as in where each line, if it is identifiable, emerges relative to the associated trochanter and side of shaft; how and where they converge to form/not form a linea aspera; the shape and surface morphology of any supra-linea aspera triangle these lines might delineate between them; where on the shaft their merging produces a linea aspera; and the degree of development and distal course of the linea aspera (personal observation).

Pickford et al. (2002) also mentioned that in BAR 1002'00 the lesser trochanter is medially projecting and, as in humans, gorillas, and *Pongo*, also well separated from the femoral neck. Regarding the latter feature, images in Pickford et al. as well as, for instance, in Robinson (1972), Day (1986), Johanson et al. (1982), and Walker and Leakey (1993) illustrate that while notable separation of lesser trochanter and femoral neck may describe specimens such as SK 82 and 97, Sts 14, AL 288-1, OH 62, KNM-WT 15000, and KNM-ER 738, 1503, and 1547, this configuration does not characterize *Homo sapiens* (or, e.g., *Pan*). Perhaps this disparity is due to differences in femoral neck length – which might imply that separation of lesser trochanter and femoral neck is phylogenetically significant not for, but within, the clade Hominidae. As discussed above, the medial orientation in BAR 1002'00 of the lesser trochanter, although similar to *Homo sapiens*, is also broadly descriptive characteristic of primates (Swindler and Wood 1973) (personal observation; see above). In contrast, in specimens such as AL 128-1, 288-1, AL 333-95, AL 333-3, Maka VP 1/1, SK 82 and 97, OH 62, KNM-WT 15000, and KNM-ER 738 and 1547, the lesser trochanter is more posteriorly than medially if not strongly posteriorly directed (Table 2).

As contemplated above, interpretation of these different configurations is not straightforward. For instance, most mammals present a medially or more medially-than-posteriorly (i.e. medioposterior to posteromedial) oriented lesser trochanter. Based on commonality, the possession of this in apes and *Homo sapiens* could reasonably be interpreted as a primitive retention – in which case configurations to the contrary would be derived and thus potentially reflect a hominid subclade. On other hand, albeit less parsimoniously (but why should parsimony always dictate interpretation?), the apparent widespread distribution among possible hominids of a posteriorly oriented lesser trochanter (and other features as well) might be primitive within a hominid clade – which implies an "independent" development of the primitive mammalian condition in *H. sapiens*. Since, however, postcrania definitively associated with crania and teeth are rare indeed, the former interpretation might be the more likely.

Another feature that Pickford et al (2002; also Galik et al. 2004) suggested unites *Orrorin* via BAR 1002'00 with australopiths and at least *Homo sapiens* is differential distribution of femoral neck cortical bone, being thinner superiorly and thicker inferiorly (Ohman et al. 1997). Taxically broader study is required.

Non-postcranial Features of "Erect Posture"

Although other postcranial features might delineate clade Hominidae, I will turn now to another skeletal region from which "erect posture" or "bipedal locomotion" has been inferred: the cranial base. For ever since Dart's (1925) discussion of the Taung child, an anteriorly placed foramen magnum with attendant occipital condyles has been central to the identification of hominoids as bipedal hominids. With *Ardipithecus ramidus* (White et al. 1994) and *Sahelanthropus tchadensis* (Brunet et al. 2002) being promoted as potential hominids, attention to basicranial morphology is crucial.

Interpretation of *Ardipithecus* (White et al. 1994) and *Sahelanthropus* (Brunet et al. 2002) as "hominid" was in part based on White et al.'s inference of bipedalism from the intersection of the bicarotid (foramen) chord and basion (=the anthropometric landmark in the midline of the anteriormost margin of the foramen magnum). The published photograph of the crushed and distorted basicranium of *Sahelanthropus* reveals, however, that what appears to be the anterior margin of the foramen magnum lies posterior to the bicarotid chord. It is obvious that in the undistorted state, the preserved left petrosal and thus the bicarotid chord were situated more anteriorly. Consequently, a forward position of the foramen magnum is not indicated.

Although not demonstrated, White et al.'s claim of an association between basion (i.e., the anterior margin of the foramen magnum) and the bicarotid chord, an anteriorly placed foramen magnum, and erect posture and bipedalism would seem intuitively reasonable. However, comparison of other potential fossil hominids, extant large-bodied hominoids, and various extant New and Old World monkeys, reveals a more complex picture (Schwartz 2004b). In juvenile anthropoids, including humans, basion, the bicarotid chord and the biporionic chord are essentially in alignment. This relationship is retained into adulthood in some anthropoid taxa, but, in others, during growth, the positions of basion and/or the bicarotid chord may change position relative to the biporionic chord. Consequently, it is the biporionic and not the bicarotid chord that better reflects the position of the foramen magnum. The alignment of basion and the two chords in the adult is, therefore, a neotenic feature that, while not defining clade Hominidae (Schwartz 2004b; Schwartz and Tattersall 2005), may be relevant to delineating relationships within it. More recently, in the context of comparison between an unspecified sample of extant catarrhines and extant *sapiens*, Kimbel et al. (2013) argued the hominid status of *Ar. ramidus* on the basis of reconstructing cranial base width and anterior foramen magnum position from missing basicranial elements in ARA-VP/500. Nevertheless, until the ontogeny of this general region in a diversity of anthropoids is understood, comparisons only between adult specimens are – as demonstrated above vis-à-vis ontogenetic changes – uninformative.

Proposed Craniodental Features of Being Hominid

Based on isolated teeth attributed to *Ardipithecus*, White et al. (1994) suggested that, in lateral profile, a hominid's permanent upper canine should present subequally long and quite divergent mesial and distal edges terminating in "shoulder-like" basal swellings that create the impression of a superoinferiorly short crown. This does not, however, describe the permanent upper canine ($C^{\backslash}$) of *Sahelanthropus* (Brunet et al. 2002) or the majority of C^1s of traditionally accepted Plio-Pleistocene and later hominids, including *Homo sapiens* (Schwartz and Tattersall 2005). Rather, White et al.'s description better captures the morphology of the $C^{\backslash}$s of adult female orangutans and the deciduous upper canines of juvenile orangutans and chimpanzees (Swarts 1988).

White et al. (1994; also Suwa et al. 2009) also described *Ardipithecus*' C^1 as "incisiform" but from the belief, also shared by Brunet et al. (2002), that a C_1-C^1-P_1 honing complex had been lost in hominids via a decrease in size and projection of these teeth (particularly the canines) in concert with closure of presumed attendant diastema. According to this scenario, as canines became less caniniform, they became associated functionally with the incisors, ultimately assuming the morphology and function of these spatulate anterior teeth. Yet, both the right C^1 allocated to *Ardipithecus* and the C^1 in the skull of *Sahelanthropus*, although differing in buccal profile triangularity, are apically pointed. Indeed, *Sahelanthropus*' trenchant C^1 would likely have occluded with a much more "caniniform"-looking C_1 than the very unprimatelike isolated element identified as this tooth (Schwartz 2004b). Although it appears from teeth in situ that *Sahelanthropus* lacked upper diastema, their absence is only inferred for *Ardipithecus* from isolated teeth. Nevertheless, if *Ardipithecus* did not have diastema, both it and *Sahelanthropus* would be more derived than geologically younger (and supposedly descendent) specimens with diastema [e.g., AL 200-1a and StW 252 (Schwartz and Tattersall 2005)] as well as the maxilla from Bouri Hata allocated to *Australopithecus garhi* [see photographs in Asfaw et al. (1999)]. Consequently, features associated with "reduction of a canine-premolar honing complex," while not defining clade Hominidae, may delineate subclades within it.

Another approach to defining Hominidae is predicated on an a priori assumption of a human-chimpanzee relationship, which immediately constrains the hominid "out-group" to this single large-bodied hominoid. Thus, although White et al. (1994, p. 306) describe the dm_1 of *Ardipithecus* as "apelike," the only ape in their comparison is *Pan*. Yet, *Hylobates* and *Gorilla* dm_1s are also very similar to *Pan* dm_1s, while *Pongo* dm_1s are most similar to those of traditionally accepted hominids, the major difference being more talonid cusp compression in the orangutan (Schwartz 2004b; Swarts 1988). Thus, *Pongo*, "australopiths," and *Homo* dm_1s conform best to White et al.'s (1994, p. 307) depiction of "apparently derived hominid features," i.e., "buccolingual crown expansion, mesiolingually prominent metaconid, well-defined anterior fovea, and large talonid with well differentiated cusps" (White et al. 1994). In fact, the dm_1s of *Pongo* and hominids[1] are similarly derived relative to other extant hominoids (Schwartz 2007b; Schwartz and Tattersall 2002, 2003, 2005): e.g., the protoconid is more mesially situated; the less vertical and lingually facing anterior fovea (= trigonid basin) is noticeably smaller than the talonid basin and is enclosed by a distinct paracristid that courses somewhat mesially and then turns toward the lingual side; and the more horizontally oriented talonid basin is enclosed by a distinct hypocristid (Swarts 1988) (personal observation).

Only if *Pongo* (and members of its clade for which dm_1s are currently unknown but for which this description would be predicted as applicable) is not the sister taxon of a potential hominid clade would these dental features be relevant to defining only clade Hominidae.

More broadly, Irish and Guatelli-Steinberg (2003) claim to have delineated features characteristic and also distinctive of the last common ancestor of clade Hominidae and also demonstrated that recent sub-Saharan Africans most closely resemble various Plio-Pleistocene hominids in these features. Their study is based on the ASU dental trait scoring system established decades ago by Turner et al. (1991) (see chapter "▶ The Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia," Vol. 3). Although seemingly objective (e.g., in matching individual dental features of a specimen with plaques of dental casts varying degrees of expression of that trait), the Turner scoring system has no relation to the terms and descriptive protocol that inform the study and systematic interpretation of mammalian teeth. Rather, Turner's system focuses instead on predefined minutiae and often idiosyncratically defined variation. Thus, although hominids are toothed mammals, Turner and scions have so ignored the

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[1] Comparison comprises juvenile *Homo*, including Melka Konturé MK81 GAR IV (2), and "australopiths" (e.g., Hadar AL 333-43b; Koobi Fora KNM-ER 820, 1477, and 1507; Laetoli LH2 and 3q; Omo 22_7; Taung; Swartkrans SK 47; Kromdraai TM1536, TM1601a, and TM1604; KB5503 and KB5223; and Sterkfontein Sts24 and StW 104 and 151).

conventions of mammalian dental terminology and description that a mammalian systematist cannot understand or even divine the morphology of the teeth subjected to the ASU scoring system. Indeed, terms such as "lower molar deflecting wrinkle" and "lower molar seventh cusp" or referring to a (huge) protostyle as an element of a "twinned hypocone" demonstrate just how far from biological/systematic practice paleoanthropology is. In short, coding for one trait after another and their presumed degrees of expression informs neither about the relations of structures to one another nor, more importantly, about the shape of a tooth and the relative expressions of as well as the spatial relationships of the details of occlusal morphology. Further, rather than testing hypotheses of which specimens might represent which morph/taxon, these analyses begin by accepting prior taxonomic allocation of specimens [e.g., (Bailey 2002, 2004; Bailey and Wu 2010; Trinkaus et al. 2000)].

Unfortunately, the emphasis of the ASU approach on scoring individual traits with a focus on degrees of trait expression (e.g., larger, larger, small, smaller; distinct, more distinct, less distinct) rather than on their relationships informed the dental "study" of specimens identified as *Australopithecus sediba* (Irish et al. 2013). Although rooting their analysis in a gorilla out-group – without understanding that gorillas are unique among large-bodied hominoids in aspects dental morphology (Schwartz 1986) – Irish et al. (Irish et al. 2013) conclude that *Au. sediba* is dentally distinct from other "hominids" but similar in a phylogenetically meaningful way to their sample of *Au. africanus* and an assumed *Homo habilis/heidelbergensis* + *H. erectus* group. The latter larger grouping is based on four features, including the vague "identical LM1 cusp 7 expression." Their conclusion, in conformity with interpretation of cranial and postcranial morphology, is that its "mosaic" of presumed primitive australopith and derived *Homo* features makes *Au. sediba* a good ancestor of genus *Homo*.

Although the taxonomic distinctiveness of *Au. sediba* has been challenged on the grounds that the skull upon which the species was based is that of subadult – and thus its adult morphology could be comparable to known specimens of australopith (Strauss et al. 2012, 2013) – tooth and mandibular morphology provide less speculative clues to understanding this hominid. Indeed, comparison with all known australopiths demonstrates that *Au. sediba* is remarkably similar to Kromdraai TM1517b, the mandibular holotype of *Paranthropus robustus* (Fig. 9).

For example, although the mandibular corpus of MH1 (UW-88-8) is more gracile, shorter superoinferiorly, and more swollen below the alveolar region – which may be because of its being subadult – both it and TM1571b are otherwise similar, including presenting two (top and bottom) mental foramina below P_1. Further, in both specimens, the anterior root of the ramus originates below the region of $M_{1\text{-}2}$, masking M_3 entirely, and then swells only modestly before becoming crest-like as it ascends, inclining a bit backward. UW-88-129 presents a moderately steep postincisal plane, as also seen in TM1517b. Damage and incomplete restoration of TM1517b preclude assessing C_1 orientation, but this tooth in UW-88-8 was relatively larger. Preserved alveoli in UW-88-8 suggest that the missing $P_{1\text{-}2}$ were similar to TM1517b in shape: i.e., P_2 was larger, especially in a distended hypocone region such that the buccal side of the tooth was mesiodistally

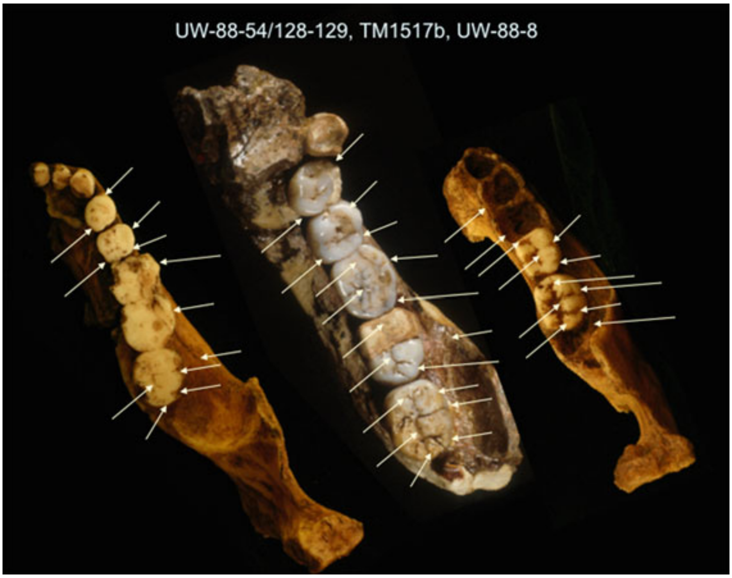

Fig. 9 Occlusal views (*left* to *right*) of right mandibles of Malapa hominid MH 2 (UW-88-54-128-129), Kromdraai TM1517b (type, *Paranthropus robustus*), and MH 1 (UW-88-8), illustrating numerous dental similarities, size being the major difference. See text for further discussion; not to scale but to relative size (Casts of MH 1 and MH 2 courtesy of the American Museum of Natural History)

somewhat shorter, while the buccal side of P_1 was marginally but still visibly longer than the lingual side. The P_2 of UW-88-129, although also smaller, is morphologically comparable to TM1517b. The M_1s of the smaller UW-88-8 and TM1517b are otherwise distinctively similar, especially in the oblique orientation of the distal part of the crown, the presence of notches between buccal cusps, and a buccal cingulid on the protoconid. Further, for example, in both UW-88-8 and the TM1517b, $M_{1\text{-}2}$ the hypoconids are compressed, they bear hypocristids, and their bases extend lingually across the midline of the crown, terminating approximately in the midline in a mesiodistally relatively long and internally squared-off end; also, small hypoconulids angle in toward the middle of the tooth, following the generally oblique orientation of their distal sides of the crowns. A groove on the internal face of the M_1 metaconid base of TM1517b produces a "pillar-like" feature, which is seen on UW-88-8's M_2. Although the mesial part of TM1517b's M_2 is partially reconstructed, the distal extremity of a definitive protoconid buccal cingulid is clearly evident abutting the mesial side of this tooth's hypoconid even in the presence of a notch between these two cusps. Similar morphological detail is noted in UW-88-8. Further, the M_3s of TM1517b and UW-88-8 are generally similar in size and shape and also in presenting buccal cusp notches (also in UW-88-55a), distinct buccal cingulids on the distal part of the protoconid, a slight buccal enamel swelling below the hypoconulid, a distobuccally obliquely oriented

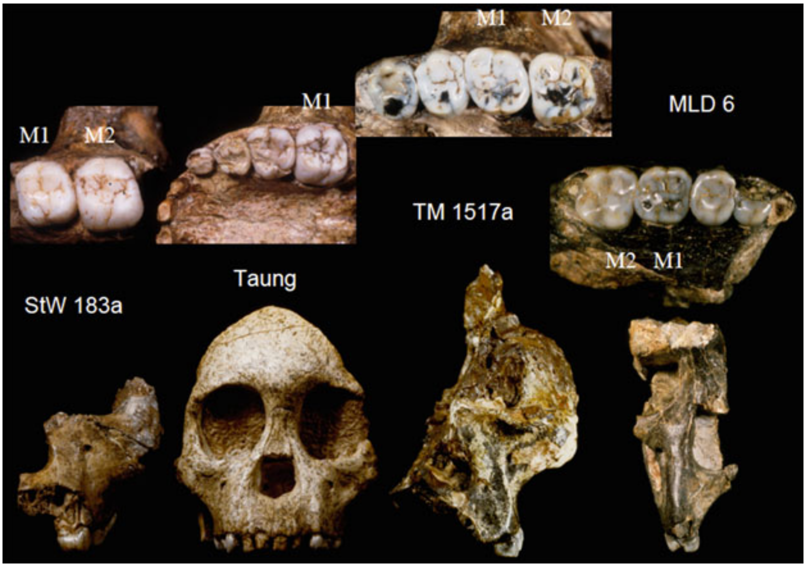

Fig. 10 Comparison of the Taung child specimen, the type of *Australopithecus africanus*, and a few other South African specimens that present similar facial and dental features of as well as variation within the Taung morph. Note that TM 1517a, which Broom referred to the holotype of *Paranthropus robustus*, compares favorably with this morph. Not to scale (Copyright © J. H. Schwartz)

metaconid base, and mesiodistally short trigonid basins confined to the inner portions of protoconid and metaconid bases.

If, as appears to be the case, these specimens represent the same hominid, they should be regarded as *Paranthropus robustus*, with the Malapa specimens' smaller size likely reflecting sexual dimorphism: i.e., MH1 was female, not male (Berger et al. 2010). Since, however, dentally and even in bony morphology the partial face TM 1517a is relatable to a morph that includes the Taung child, and which therefore must regarded as *Australopithecus africanus* (Schwartz and Tattersall 2005; Fig. 10), only the lower jaw from Kromdraai TM1517b represents the holotype of *P. robustus*. In this regard, future comparisons of the upper dentition of MH1 with those of other "australopiths" should prove enlightening in sorting out which specimens actually do represent this taxon. Certainly, we now know a lot about the postcranial skeleton of this hominid.

Additional Defining Characters of Hominidae

Although some obviously derived features when considered in isolation might delineate clade Hominidae, they are also shared with *Pongo* and its potential extinct relatives. Consequently, in order to claim them as strictly hominid apomorphies, and their presence in an orangutan clade as autapomorphic for it and non-synapomorphic with hominids (i.e., features seen in hominid and orangutan clades are homoplastic), one must first embrace another theory of extant large-bodied hominoid relationship and then "explain away" the phylogenetic significance of the similarities between humans and orangutans, which is often done merely by declaring them homoplastic (e.g., Collard and Wood 2000, 2007; Diogo and Wood 2011; Lockwood and Fleagle 1999; Wood and Harrison 2011) as if homoplasy were identifiable without first presuming a theory of relationship based on characters deemed synapomorphic for other taxa (see discussion in Schwartz 2008; see also chapter "▶ Homology: A Philosophical and Biological Perspective," Vol. 1).

This, of course, is the current state of affairs in paleoanthropology, wherein the molecular similarities between *Pan* and *Homo* are taken as evidence of their close relationship (e.g., see Lockwood et al. 2004; Pilbeam 1986, 2000; Gibbs et al. 2000, 2002; Wood and Harrison 2011), even though most of the "favorable" comparisons involve only small portions of the 2–3 % coding (i.e., metabolically, not developmentally relevant) region of the genome and rarely include the orangutan and an array of other catarrhines (e.g., Grehan and Schwartz 2009; Grehan and Schwartz 2011; Schwartz 2009, 2011, 2012; Schwartz and Maresca 2006). Although Wood and Harrison (2011) assert there is also "overwhelming. . .morphological evidence for a ((*Pan*, *Homo*) *Gorilla*) *Pongo*) pattern of relationships" and that features suggesting a *Pongo*-*Homo* sister group were "selected" to do so (p. 470), neither of these statements is correct, especially, "overwhelming-morphological evidence for with regard to a ((*Pan*, *Homo*) *Gorilla*) *Pongo*) pattern of relationships." Although Groves (1986) is consistently cited as having demonstrated a close human-chimpanzee relationship, scrutiny of his data demonstrates not only that most of the features he presented in support of this contention are not synapomorphic because they are found in other primates listed (Grehan and Schwartz 2009; Groves 1986; Schwartz 1988, 2005) but, more importantly, that numerous features are either ambiguously or incorrectly reported (Grehan and Schwartz 2009).

Unfortunately, Groves' work has been reiterated without question in subsequent publications claiming demonstration of a *Homo*-*Pan* relationship (e.g., see especially Lehtonen et al. 2011; Strait and Grine 2004; Collard and Wood 2000; Gibbs et al. 2000, 2002). Further, in light of Wood and Harrison's claim of "overwhelming. . .morphological evidence for a ((*Pan*, *Homo*) *Gorilla*) *Pongo*) pattern of relationships," Wood's own work (Collard and Wood 2000; Gibbs et al. 2000, 2002), which was based in large part on Groves (1986), delineated essentially no hard-tissue and only a handful of soft-tissue features in support of a human-chimpanzee sister group. With regard to the criticism that features in support of a human-orangutan sister group were selected to demonstrate this, scrutiny of the relevant publications reveals that in all cases the comparative morphological, physiological, and developmental data cited was available in the literature (Grehan and Schwartz 2009; Schwartz 1983, 1988, 2004a, 2005). When new data was introduced, it was spelled out and, as with all data, presented for an array of primates, not just humans and large-bodied hominoids (Grehan and Schwartz 2009; Schwartz 1983, 1988, 2004a, 2005). In contrast to Groves' claiming

Homo-Pan synapomorphy not only in the rare instances when only these two hominoids shared features but more frequently when other primates shared features present in humans and chimpanzees, I hypothesized synapomorphy only when two taxa exclusively shared a feature. Consequently, in every publication, I presented all alternative theories of relationship, including *Homo-Pan*, even though they differed significantly in degree of robustness (= corroboration). The fact of the matter is, even if one used Groves' data without eliminating ambiguous or incorrect data, and hypothesized synapomorphy on the basis of exclusivity of shared features, *Homo-Pan* emerges as the least and *Homo-Pongo* as the most highly supported theory of relationship (Schwartz 1988). With the addition of more features to the data base, and in the context of a broad comparison among primates, the same pattern of relationship emerges (Grehan and Schwartz 2011). If one were to cast the stone of "selectively" choosing features to support a particular human-ape theory of relationship, it would have to be toward those who maintain a *Homo-Pan* sister group through reiteration of faulty morphological datasets and ignore additional data that might lead to a conclusion other than their preferred conclusion.

Nevertheless, even if the latter phylogenetic hypothesis were true, this does not justify using *Pan* alone as the referent for defining clade Hominidae or for determining character polarity within this clade (e.g., see Asfaw et al. 1999; Brunet et al. 2002; Guy et al. 2005; Lovejoy et al. 2009b, c; Suwa et al. 2009; White et al. 1994, 2006; Wood and Harrison 2011). Rather, the broad comparative approach that Le Gros Clark might have pursued remains the more reliable way in which to hypothesize features that could distinguish a hominid from other primate clades and also determine character polarity within it. And, in doing so, one must also confront instances when humans, or hominids in general, compare more favorably with primates other than *Pan*, as, indeed, they often do with *Pongo*.

Pongo-like Dental and Palatal Features of Potential Hominids

An interesting case of "interpreter's bias" lies in analyses of molar enamel thickness. For example, although Martin (1985) has been cited as demonstrating that the last common ancestor of large-bodied hominoids had thick molar enamel (which was retained in orangutan and hominid clades but secondarily reduced in African apes), he merely interpreted enamel thickness data in the context of an [orangutan (human-African ape)] theory of relatedness (Schwartz 1987). Otherwise he should, or at least could, have concluded that thick molar enamel united human and orangutan clades. Kelley and Pilbeam (1986) also interpreted molar enamel thickness in the context of an [orangutan (human-African ape)] theory of relatedness but presented two scenarios: Martin's and one in which the last common ancestors of separate human and orangutan clades independently developed thick molar enamel. In the latter case, thick molar enamel would be a defining feature of Hominidae. In contrast, but embracing first a human-chimpanzee relationship, Suwa et al. (2009) could claim that thin enamel was secondarily derived in *Pan*.

More recently, Schwartz (2000) found that, while humans and orangutans both have thick molar enamel, humans have thicker enamel in some areas of their occlusal surfaces. He suggested that thick molar enamel had evolved independently in humans and orangutans (and, by implication, in the last common ancestors of separate human and orangutan clades) because of the demands of different diets. A more straightforward interpretation of G. Schwartz's data is that human and orangutan clades shared a thick-molar-enameled common ancestor and that, within this clade, humans (and perhaps other hominids) are more derived. Only by accepting thick molar enamel as synapomorphic of traditionally accepted hominids can one embrace thin-enameled *Ardipithecus* as a sister of this clade (assuming that this relationship is based on synapomorphy). Of course, Brunet et al.'s (2002) suggestion that the thicker enameled *Sahelanthropus* is ancestral to *Ardipithecus*, and Suwa et al.'s (2009) argument based on a presumed hominid-*Pan* sister group that thin enamel in the latter must be secondarily derived, underscores the need for systematic rigor in paleoanthropology. For, indeed, explaining the distribution of morphology based on an already accepted theory of relationship does not substitute for the generation of that theory.

If thick molar enamel does not contribute to defining Hominidae, does dental morphology? Some aspects of it might (e.g., see discussion above on dm_1 morphology) but, at present, delineating more than a handful of features would be a Herculean task. This difficulty derives from the longstanding notion of the Miocene being a time of an "ape radiation," after which "hominids" emerged. Guided by this scenario, paleoanthropologists typically identified post-5.5 ma specimens with thick-enameled cheek teeth as "hominid" and pre-5.5 ma specimens as orangutan relatives. Nevertheless, study of fossils identified as hominid reveals that *Pongo*-like teeth have often been referred to species of *Homo* and *Australopithecus* (Grine and Franzen 1994; Schwartz 2004a; Schwartz and Tattersall 1996). Teeth allocated to *Orrorin tugenensis* (Senut et al. 2001), if truly thick-enameled, reinforce the question of how many Miocene "apes" are actually hominids and how many Plio-Pleistocene "hominids" are not. In addition, since "hominid" teeth are often worn flat, little attention has been paid to details of occlusal morphology. Thus, although most of the human fossil record has now been scrutinized at the level of morphs (Schwartz and Tattersall 2002, 2003, 2005), much work on testing these hypotheses remains before assigning specimens (other than, of course named type specimens) to specific genera and species.

Were it not for their presence in, for instance, *Pongo*, *Sivapithecus*, and *Ankarapithecus*, other features that could "define" Hominidae are the development of a single incisive foramen (Schwartz 1983, 1997) and a posteriorly thickened palate (as seen in midline cross section) (Schwartz 2004a). With regard to the palate, if the Hadar broken palate AL 200-1a does thin posteriorly, it would be the outlier among "accepted" hominids (Schwartz 2004a; Schwartz and Tattersall 2002, 2003, 2005). As with thick molar enamel and the morphological details of dm_1, the simplest phylogenetic interpretation of these features is that they characterized the last common ancestor of human and orangutan clades.

Pongo-Like Features of "Australopiths": Implications for Defining Hominidae

Another stumbling block to defining Hominidae is the degree to which "australopiths" and specimens traditionally allocated to *Homo* differ from one another, especially in craniofacial morphology, e.g., in orbital and nasal aperture outline as well as in the configuration of the supra- and infraorbital regions; elevation of the nasoalveolar clivus above the floor of the nasal cavity; height and orientation of the subnasal region; orientation, flatness, and height of the zygomatic region; development of a "snout" with/without facial pillars (vertical or medially inclined); and a canine fossa, and in the development and configuration of a mastoid process. Thus, while one might unite all of these potential hominids via various postcranial features, craniofacial morphology seems only to delineate possible hominid subclades. This may in part explain why one approach to associating living humans with *Pan* is to try first to link the latter with australopiths and then to assert, since australopiths and *Homo* form a clade, that humans and chimpanzees are closely related (Begun 1994; Begun et al. 1997). In the latter case, the primary feature of supposed synapomorphy between (an undefined) *Australopithecus* and *Pan* – bar-like supraorbital torus with sulcus behind – describes no "australopith" (e.g., Figs. 10 and 11) and only some specimens of *Homo* (e.g., Fig. 13; Clarke 1987; Schwartz and Tattersall 2002, 2003, 2005). In addition, not only is the markedly inferosuperiorly tall supraorbital region of *Sahelanthropus* not bar-like as in African apes [i.e., it is not both superiorly and slightly anteriorly projecting and bound posteriorly by a distinct posttoral sulcus; see Schwartz (1997) for discussion], it is so unusually tall that it must represent a derived, not primitive, configuration – which, together with its distinct dental morphology and not very thick molar enamel, makes determining its relationship to any hominid (or ape) difficult indeed (Schwartz 2004b).

While seeking connections between fossil hominids and African apes (especially *Pan*) has historical precedent (Johanson and White 1979), the most favorable comparisons are actually between *Pongo* (and its fossil relatives) and australopiths and some specimens attributed to *Homo* (Grehan and Schwartz 2009; Schwartz 2004a, 2005), e.g., rim-like superior orbital margins with a rather smooth transition into the frontal plane; often ovoid orbits; and forwardly facing, tall, and often vertical zygomatic regions (a further derived configuration, e.g., as in KNM-WT 17000, is a posteriorly tilted zygoma) (Figs. 10, 11, 12, and 13). Since the faces of *Pongo*, *Sivapithecus*, and *Ankarapithecus* as well as of most specimens taken as being hominid are relatively tall superoinferiorly and, even with anteriorly oriented zygomas, relatively narrow from side to side, those specimens with broad and short faces (in the orangutan clade, *Lufengpithecus* and among hominids, e.g., AL 444-1, SK 48, KNM-ER 406, KNM-WT 17000, KNM-ER 3883) emerge as potentially derived, which for hominids may reflect relatedness among some, if not all of them (see also Schwartz and Tattersall 2005; Fig. 14). Many australopiths are also similar to *Pongo* in having distinct facial pillars that emerge just above the canines and, together with a variably developed canine fossa, delineate a "snout" [Figs. 10 and 11; see also

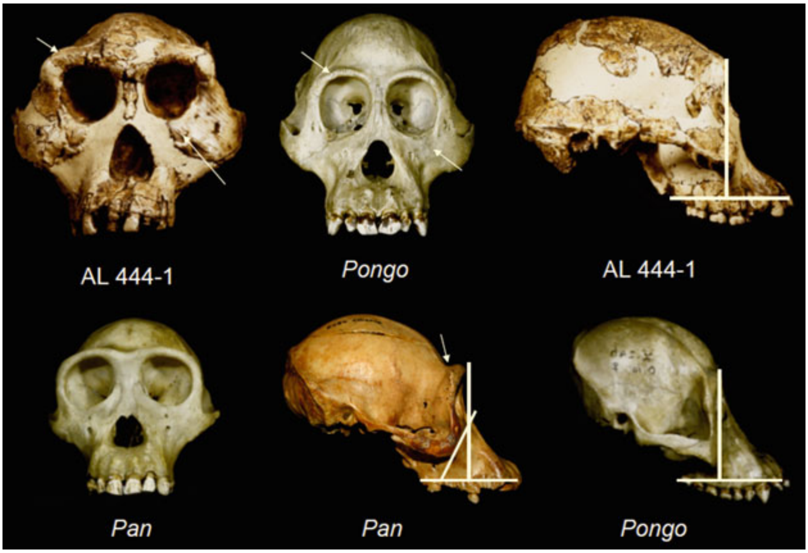

Fig. 11 Comparison of AL 444-1 (cast of reconstruction) with *Pongo* and *Pan* illustrating lack of *Pan*-like supraorbital, lower facial, and zygomatic morphology, but orangutan-specific features in the hominid. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

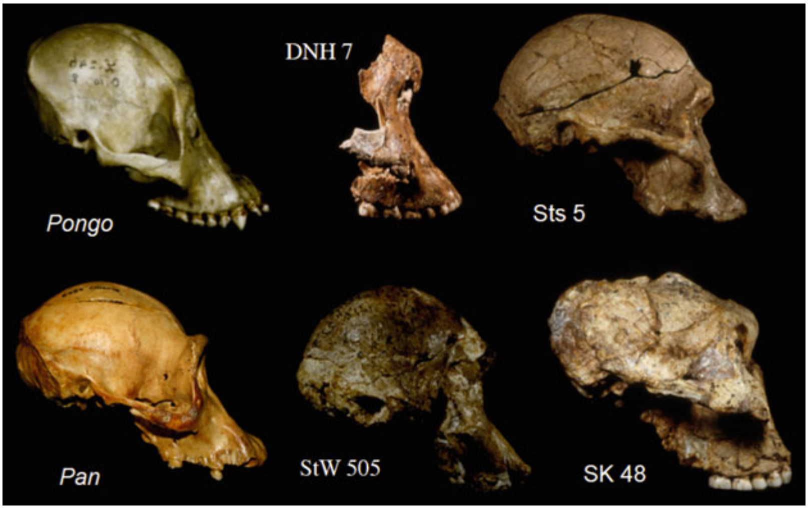

Fig. 12 Right lateral views of *Pongo*, Drimolen DNH 7, and Sts 5 (*top row*) and *Pan*, StW 505, and SK 48 (*bottom row*) illustrating, e.g., lack of *Pan*-like supraorbital, lower facial, and zygomatic morphology but orangutan-specific features in the hominids. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

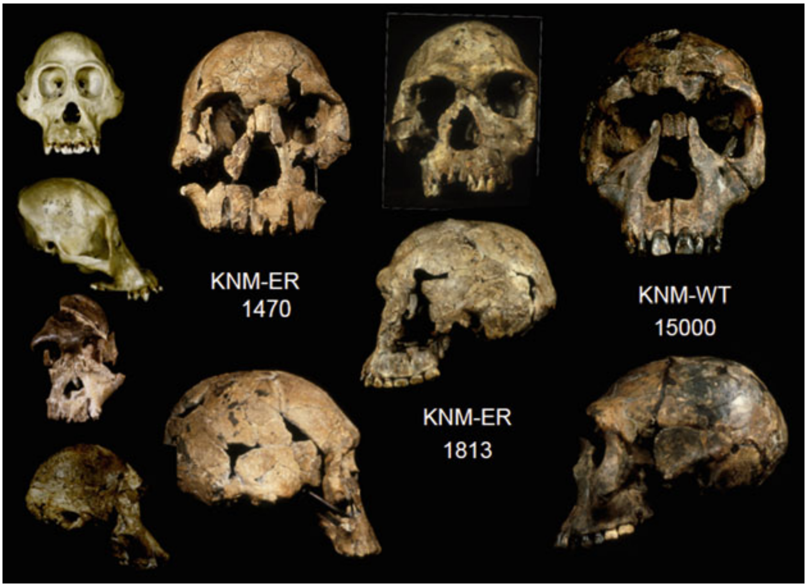

Fig. 13 Comparison of (*left column*) *Pongo* and StW 505 with various specimens allocated to *Homo* illustrating especially orangutan-like facial features. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

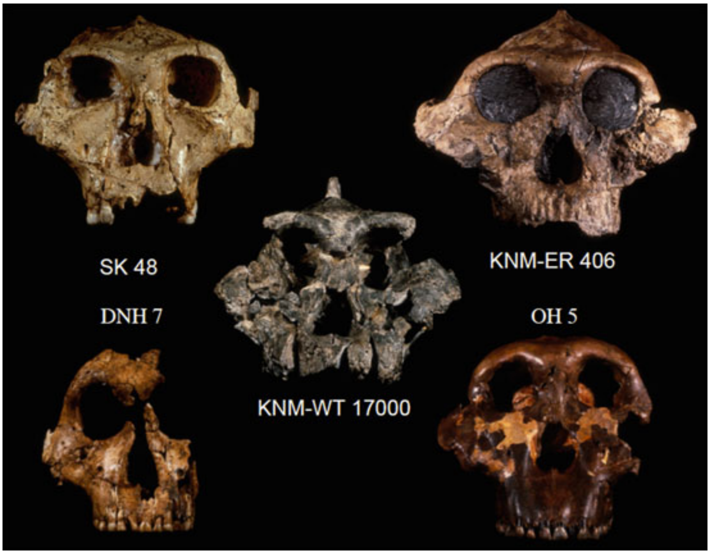

Fig. 14 Comparison of various specimens of "robust australopith" to illustrate similarly derived laterally broad and superoinferiorly short faces in SK 48, KNM-ER 406, and KNM-WT 17000, which might reflect their membership in a hominid subclade that does not include specimens such as DNH 7 and OH 5. See text for further discussion; not to scale (Copyright © J. H. Schwartz)

illustrations in Schwartz and Tattersall (2005)]. Interestingly, the Taung specimen has the long, slit-like single incisive foramen seen in *Pongo* and also preserved in *Sivapithecus* and *Ankarapithecus* (Schwartz 2005). While I am not advocating a special relationship between a *Pongo* clade and some or all australopiths, attention to these apparent synapomorphies is more relevant to the task of defining Hominidae, its subclades, and sister taxa than is currently appreciated.

Indisputable similarities between *Pongo* and australopiths exist (Schwartz and Tattersall 2005) and they should be accounted for in any critical evaluation of human-ape and within-hominid relationship. Further, these similarities make even more critical for defining a hominid clade and relationships within it broadening comparisons from solely between hominids and *Pan* alone, or between hominids and both African apes, to include as many catarrhine taxa as possible in order to provide the best foundation for delineating shared character similarity and determining character polarity – which are critical to phylogenetic reconstruction.

Conclusions

When comparing extant taxa, defining Hominidae is a simple matter. Through a curious historical twist, *Homo sapiens* is the only survivor of a clade whose dimensions we will never fully know. Take, for instance, the discovery of an apparent hominid from the late Pleistocene of Flores, Indonesia, best seen in LB1 (Brown et al. 2004). Its combination of morphologies would be unexpected no matter what its age.

LB1 has or had a moderately globular cranium (as in some hominids); somewhat thickened and anteriorly (but not superiorly) protruding but rim-like supraorbital margins with no sulcus behind (australopiths in part and orangutans and their relatives); tall, ovoid orbits (*Pongo*, *Sivapithecus*, some “australopiths”); flat nasal bones (most hominoids, including some *Homo*); forwardly facing and vertical yet superoinferiorly short zygomas (australopiths and orangutans and their relatives); well-developed mastoid processes (some “australopiths” and some *Homo*); a thick frontal with thick diploe (autapomorphic or pathological); no frontal sinuses (most primates, including bonobos); an anterior cranial fossa that does not extend fully over the orbital cones (most primates, including some *Homo*); a clivus that slopes gently away from the dorsum sellae (most primates, including some *Homo*); basion and bicarotid and biporionic chords in alignment (juvenile anthropoids, some adults); a broad incisive foramen that proceeds anteriorly as a expanding groove (a few “australopiths,” e.g., OH 5); marked separation of the nasoalveolar clivus and an anteriorly thin palate (African apes, some Miocene hominoids, some “australopiths”); a smoothly but narrowly curved mandibular symphyseal region (many anthropoids); a long retromolar space (various *Homo*); a broadly and smoothly rounded but somewhat truncated gonial angle (some *Homo*); a very anteroposteriorly long sigmoid notch (some *Homo*); a sigmoid notch crest that is deepest near the coronoid process (autapomorphic); very large cheek teeth and apparently relatively small anterior teeth (some “australopiths”); unusually mesiodistally short upper and lower molars with large mesial and truncated distal cusps (autapomorphic); a relatively long ilium (e.g., SK 50) with a beaklike anterior superior iliac spine (great apes, SK 50, MLD 7 and 25); a poorly defined iliac pillar (australopiths); a knoblike anterior inferior iliac spine that lies noticeably superior to above and somewhat back over the supra-acetabular rim (hominids as discussed here); an arcuate line that descends well before reaching the region of the acetabulum (some hominids); no ischial spine (most primates); posterior iliac expansion that defines a greater sciatic notch (hominids as used here); a "V"-shaped greater sciatic notch (most hominids, but not Neanderthals); a large femoral head (most primates); a long and anteroposteriorly compressed femoral neck (*Orrorin*, "australopiths" including BOU-VP-12/1, and some *Homo*, e.g., OH 62, KNM-WT 15000, D4167); a well-defined intertrochanteric crest (most primates, but not KNM-WT 15000, *Orrorin*, and most if not all "australopiths" or OH 62); a medially facing lesser trochanter (most primates, not "australopiths" or various *Homo*, e.g., OH 62, KNM-WT 15000, D4167); a weakly developed linea aspera (*Orrorin* and various "australopiths"); a femoral "carrying angle" ("australopiths" and *Homo*); a tibia that is much shorter than the femur (at least apes); poorly differentiated tibial tubercles (most primates); a medial tibial condylar facet that is situated higher than the lateral (at least apes); and a convex medial tibial facet (apes and some "australopiths," e.g., AL 288-1a, AL 129-1b) (see Brown et al. 2004).

Is this Flores specimen – if the cranial and postcranial remains represent a single individual – a hominid? A gut reaction based on the external morphology of the skull is "yes," but the internal morphologies are odd. The teeth are not necessarily hominid, the humeral shaft lacks the torque or "twist" characteristic of large-bodied hominoids (Morwood et al. 2005) and the morphology of the distal articular region is clearly not hominoid (Morwood et al. 2005; Schwartz 1986), the tibia is definitely not hominid, the femur is *Orrorin*-like, and the partial os coxa is somewhat "australopith"-like. So why is the composite Flores specimen considered a species of *Homo* when its affinities to a clade Hominidae are not entirely clear? Largely because there has been a history of allocating specimens to taxa based more on their geological age than on their morphology – which, in turn, has led to the general practice of trying to explain away "anomalous" morphologies in terms of variation (see also chapter "▶ General Principles of Evolutionary Morphology," Vol. 1). Methodologically, however, before one even contemplates referring a specimen to a genus and species, one should have to defend first why any specimen is a hominid and then a member of the nested subclades that subsume that species (see also chapter "▶ Principles of Taxonomy and Classification: Current Proce dures for Naming and Classifying Organisms," Vol. 1). But in order to do so, we must have a working definition of this potential clade that is open to criticism, testing, and revision, rather than constructed in the context of a presumed theory of hominid-ape and then hominid-subclade relationship, wherein primitive features dominate the description and homoplasy assumed demonstrable (Lovejoy et al. 2009a; Wood and Harrison 2011). In this regard, there is still much work to be done.

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Defining the Genus *Homo*
- ▶ Fossil Record of the Primates from the Paleocene to the Oligocene
- ▶ General Principles of Evolutionary Morphology
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Later Middle Pleistocene *Homo*
- ▶ Origin of Bipedal Locomotion
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Species and Diversity of Australopiths

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Role of Environmental Stimuli in Hominid Origins

Elisabeth S. Vrba

Contents

Abstract

Environmental stimuli have influenced the evolution of hominins and other mammals at the levels of ontogeny, organismal adaptation, and speciation. The review refers to some agreement which has emerged – as well as to

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E.S. Vrba (✉)
Department of Geology and Geophysics, Yale University, New Haven, CT, USA
e-mail: elisabeth.vrba@yale.edu

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persistent debates – on the issue of environmental linkages to hominin adaptation. Current hypotheses which link physical change, adaptation, and speciation in general and in hominins in particular are discussed (including hypotheses on the role of ecological specialization and generalization, the coordinated stasis and variability selection hypotheses, habitat theory, and the turnover pulse hypothesis). Some persistent debates are revisited (such as on the current status of the savanna hypothesis and on whether or not there was mammalian species' turnover in the Turkana Basin during the Plio-Pleistocene). The relation of hominin evolution to the recent finding of several turnover pulses coincident with global cooling trends in the 10 Ma to recent record of all African larger mammals is considered. One example of hypotheses which address issues of environmental stimuli of ontogenetic evolution is the heterochrony pulse hypothesis: the generative properties shared among lineages can result not only in coherence of morphological changes but also in a strongly nonrandom timing of heterochrony events, as diverse lineages respond in parallel by similar kinds of heterochrony to the same environmental changes. The discussion includes cases in hominins and other mammals of evolutionary increase in body size by prolongation of growth and attendant "shuffling" of body proportions including relative increase in brain volume, namely, encephalization.

Introduction

It is a truism that environmental stimuli have influenced the evolution of hominins and all other life forms. The challenge is to understand the causal subcategories: what are the hypotheses and predictions that should be tested and what kinds of data can be used to best effect. This approach is based on three premises: (1) one needs to study not only the hominins but also their wider biotic and environmental contexts. (2) Given the aim of understanding hominin evolution, the theory of evolution should be accorded more prominence than has been the norm, and an expanded theoretical framework is needed. A focus on the dynamics that link the environment to selection and adaptation at the organismal level is insufficient. One also needs to consider the causal linkages from the environment to dynamics at lower and higher levels – from morphogenesis during organismal ontogeny to the macroevolutionary level of species turnover (speciation and extinction) – and investigate the separate and combined roles in the origins of new phenotypes and species. (3) The direct influence of physical environmental stimuli on evolution at each level deserves more intensive study than it has been accorded traditionally. For much of the century following Darwin (1859), the research disciplines of geology (including climatology) and paleobiology were conducted separately. Speculations abounded on how they might link, but analyses directly integrating data from both areas remained sparse. This changed over the past decades as more refined methods led to discovery of new patterns and causal principles in paleoclimatology (e.g., the astronomical climatic cycles, Hays et al. 1976) and in the fossil record (e.g., rigorous phylogenetic hypotheses, geochemical inference of past diet, etc.). Proposals that hominins, the beginning of bipedalism, and other important human adaptations occurred in the African savanna, in response to the new selection pressures in such more open environments, are often loosely grouped under the term "savanna hypothesis." The first such proposal is often attributed to Dart (1925) who wrote (pp. 198–199), for example, that in the ancestral forest,

> Nature was supplying with profligate and lavish hand an easy and sluggish solution....For the production of man a different apprenticeship was needed to sharpen the wits and quicken the higher manifestations of intellect – a more open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderant role in the preservation of the species.

Later notable examples include the dietary hypotheses of Robinson (1963) and Jolly (1970). In his insightful review, Potts (1998b:107) considered that "Washburn's [1960 and other publications] influence and interest in intrinsic accounts (as opposed to extrinsic accounts, which interpreted evolutionary events in relation to environmental change) may explain why many paleoanthropologists in the 1950s–1970s paid little attention to environmental context." Early papers proposing physical change as a direct cause of hominin evolution concerned particular stratigraphic sequences in East and southern Africa (respectively, Coppens 1975; Vrba 1974, 1975; both compared climatic indications from mammalian change with the hominin record), the circum-Mediterranean area (Hsu et al. 1977 implicated the Messinian Salinity Crisis in hominin origin), and comparison of global climatic data with the hominin record (Brain 1981a).

Darwin (1859) argued that the initiating causes of phenotypic change and speciation are located at the level of organisms, namely, natural selection, particularly arising from competition: ".... each new species is produced . . . by having some advantage over those with which it comes into competition . . ." (p. 320). He stressed climatic effects on competition rather than on population structure: "in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals...." (p. 68). Darwin thought that an understanding of organismal selection and adaptation will also answer the question of species' origins. Most later evolutionary studies, including those in paleoanthropology, have continued in this tradition. (See Tattersall 1997a who argued that "paleoanthropology fell completely under the sway of the evolutionary views of the [neoDarwinian] Synthesis – where it remains, for the most part, today.") The questions which will be addressed, using theory and evidence, include how physical dynamics have influenced species' structure and speciation, organismal ontogenetic systems, and selection and adaptation. I also consider some of the interactions among these levels.

Hominini means the evolutionary group of species which are considered by most to be more closely related to humans than to chimpanzees. The term "species" is used for a sexually reproducing lineage, the members of which share a common fertilization system, and "speciation" for the divergence of the fertilization system in a daughter population to reproductive isolation from the parent species

(Paterson 1982), with awareness of the difficulties involved in applying such concepts to the fossil record (Kimbel 1991; Vrba 1995a). The terms "habitat," "specific habitat," and "habitat specificity" of an organism or species refer to the set of resources that are necessary for life; resources are any components of the environment that can be used by an organism in its metabolism and activities, including ranges of temperature, relative humidity and water availability, substrate characteristics, places for living and sheltering, and all kinds of organic foods such as plants and prey, mates, and other mutualist organisms in the same or different species (Vrba 1992). An organism's biotic environment derives from other organisms and biotic interactions such as competition, parasitism, predation, and mutualism. "Physical change" refers to the global and local effects from extraterrestrial sources, including the astronomical climatic cycles, and from dynamics in the earth's crust and deeper layers as manifested by topographic changes such as rifting, uplift, sea level change, and volcanism. The use of the term "savanna" follows Ratnam et al. (2011) and Cerling et al. (2011:53): "a modern ecological definition of the term savannah is comprehensive and includes structural, functional and evolutionary aspects, Ratnam et al. 2011. Because our focus is on reconstructing the physiognomic structure of palaeo-vegetation, we use a purely structural definition of savannah [quoting Ratnam et al. 2011]: "mixed tree-grass systems characterized by a discontinuous tree canopy in a conspicuous grass layer.""

Physical Change, Adaptation, and Speciation: Some Current Hypotheses

The traditional hypothesis follows Darwin closely and has often been called neoDarwinian. In its most conservative form, it assumes that adaptation and speciation are always driven by natural selection. The particular causes of selection are seen as very diverse, the most important being organismal interactions – such as competition and predation – that can act alone, or in combination with physical change, to initiate and complete speciation (and extinction). Under this null hypothesis, H_0, selection pressures that cause speciation, differs from group to group and from one local area to the next. To explore how this model's predictions differ from others, let us ask: what rhythm of speciation events would one expect if we could see all the events in the real world across the entire area under study (e.g., Africa) and if we plotted their frequencies against time? H_0 predicts that the pattern of origination frequencies for large areas, over long time, is a random walk in time with an averagely constant probability of origination. Examples of such arguments are found in Van Valen (1973), Hoffman (1989), McKee (1993), and Foley (1994). In contrast, a number of hypotheses share the argument that physical change has an important causal role in initiating the evolution of novel adaptations and species turnover, with the consequent prediction that such evolutionary events should be nonrandomly distributed in time and in association with episodes of physical change. Several such hypotheses will be discussed after introducing some relevant theory.

Allopatric Speciation

Allopatric speciation occurs in isolated populations that have been separated by vicariance or dispersal over barriers. (Vicariance is the fragmentation of a formerly continuous species' distribution into separated populations.) Gulick (1872), who studied the Hawaiian fauna, was the first to argue that the causes of speciation are not well explained by selection among competitors, but that vicariance brought about by physical changes was seminal in initiating speciation. Mayr's (1942, 1963) comprehensive arguments for allopatric speciation eventually resulted in widespread agreement that this mode predominates. Although there continue to appear claims of sympatric speciation, mainly in herbivorous insects and fishes, most recent such reports acknowledge that the best evidence remains circumstantial (review in Vrba 2005). It is fair to say that an expectation of predominant allopatric speciation, particularly in hominins and other large mammals, is consistent with the weight of available evidence and enjoys widespread consensus. In terms of earlier concepts of hominin phylogeny, which accepted a progression from the earliest biped to *Homo sapiens* with minimal branching from that lineage, one might wonder whether it is worthwhile to test causal hypotheses of hominin speciation, but recent finds indicate that "any accurate view of ourselves requires recognizing *Homo sapiens* as merely one more twig on a great branching bush of evolutionary experimentation" (Tattersall 1999:25, 2000). That is, we need to consider seriously the question of what caused lineage branching in the hominin tree.

Physical Change as the Driver of Vicariance, Selection, and Speciation

If allopatric speciation predominates, then so also must physical initiation of speciation predominate. Vicariance is nearly always produced by tectonic and climatic change. Incipient speciation initiated by dispersal over barriers also in most cases implies the causal influence of physical change (e.g., chance *Drosophila* fly dispersals over the ocean always occur, whether there are islands within reach or not; it took the production of the precursor islands of the Hawaiian Archipelago for the founding of those first allopatric populations of Hawaiian drosophilids, Carson et al. 1970). Thus, the chief causes of population size reduction and allopatry in the history of life have probably derived from physical changes. Although the relationship of punctuated equilibria to physical change was not explored in Eldredge and Gould (1972), the pattern they argued for implies independently that the initiation of speciation mostly comes about through physical change (Vrba 1980): if species are in equilibrium for most of their durations, what causal agency of the punctuation can one invoke other than physical change? The general consensus on the importance of allopatric speciation, together with the implications of punctuated equilibria and Paterson's (1978) "recognition concept" of species, led to the proposal that physical change is required for most speciation (Vrba 1980). Paterson (1978, 1982) argued that change in the fertilization system, the critical evolutionary change in sexual speciation, is most likely to occur in small, isolated populations that are under selection pressure from new environmental conditions.

Ecological Specialists and Generalists

This contrast is of general evolutionary interest (Stebbins 1950; Simpson 1953; Eldredge 1979; Vrba 1980, 1992) and particularly germane to mammalian evolution during the climatic instability of the late Neogene (Vrba 1987a). It has been discussed using various terminologies, such as stenotopy and eurytopy (e.g., Eldredge 1979), niche breadth (e.g., Futuyma 1979), and breadth of habitat specificity or resource use (Vrba 1987a). Specialist and generalist adaptation can be expressed in relation to different kinds of environmental variables, e.g., with respect to food intake, temperature, vegetation cover, light intensity, etc. Given the effects of the late Neogene climatic and tectonic changes in Africa (see sections "Physical Background: Climatic Change" and "Physical Background: Tectonism"), the distinction between species which are stenobiomic (restricted to a particular biome) and eurybiomic (ranging across biomes) is particularly relevant. As populations of a species encounter a new environment, beyond the ancestral biome range, they could in principle either diverge from their adaptation to the ancestral biome to become specialized on the new one or become more eurybiomic by broadening their resource use to include the new biome alongside the ancestral one (e.g., Vrba 1987a, 1989a). Evolution toward eurybiomy, which is very rare (e.g., Hernández Fernández and Vrba 2005 found a large preponderance of biome specialists in living African mammals), is of special interest as it applies to *Homo* (Vrba 1985a, 1989a; Pickford 1991; Potts 1998a; Wood and Strait 2003). Proposals that temporal and/or spatial environmental variability, namely, life in fluctuating or unpredictable environments, can promote generalist adaptations have a long history of extensive discussion (e.g., Stevens 1989 reviewed the evolution of broad climatic tolerance in high-latitude environments which have a greater range of annual and longer-term variation). Adaptations to strong seasonality range across life forms, from diatoms and other photosynthetic groups in polar waters (which each winter form resting spores in response to darkening and sink down dormant out of the plankton environment to germinate again when light returns, Kitchell et al. 1986) to the deciduous habit of many plants and hibernation and long-distance migration in animals. In advanced vertebrates, complex behaviors form an important category of such adaptations, ranging from the behavioral adjustments of animals to changing temperature and aridity (Maloyi 1972) to hominine culture.

The notion of a "biome generalist species" can be subdivided as follows. The eurybiomic phenotypes can be either (A) heritable, namely, genetically based and fixed, or (B) expressed as ecophenotypes, within a broad norm of reaction, in response to varying environments (Hall 2001; West-Eberhard 2003). Case (A) has two subcases. A1: Each organism can live in more than one biome, either because each organism has the needed biomic flexibility or because each organism is a specialist on resource patches which occur across biomes. An example of the latter is the aardvark, *Orycteropus afer*, which is stenophagous (it eats only ants and termites), a substrate specialist (it digs burrows in sandy or clay soil), and stenophotic (it is nocturnal). Yet *O. afer* is eurybiomic: its specialized “resource patches” range from semidesert to dense, moist woodland across Africa. A2: There are intraspecific differences in resource use among organisms and populations; i.e., polymorphism in resource use allows the species to respond to environmental fluctuations by shifting relative abundances of the variants. An example is the African buffalo (Sinclair 1977): *Syncerus caffer caffer* differs in phenotype and resource use from (and lives at higher latitudes and/or altitudes with more grassland present than) the smaller, plesiomorphic phenotype *S. c. nanus* (in warm, forested regions). This species appears to have “rolled with the punches” of large and frequent climatic changes since the late Pliocene mainly by changes in polymorphic frequencies. All generalist adaptations first evolve in populations, thus rendering the species polymorphic. Intraspecific adaptations and polymorphisms, which become more elaborate with repeated climatic shifting, are likely to be the most frequent responses to climatic extremes (see Vrba 1992: Fig. 4c) with speciation and extinction being rarer outcomes.

Habitat Theory and the Turnover-Pulse Hypothesis

The turnover-pulse hypothesis is a part of the broader “habitat theory” which focuses on species’ habitats and on the dynamic relationships between physical change, habitats, and species (Vrba 1985b, 1992). It uses the predominance of allopatric speciation and the consequence that physical change is required for most speciation. Climatic changes (from global or/and local tectonic sources) result in removal of resources from parts of the species’ former geographic distributions and therefore in vicariance. Vicariance on its own is insufficient for speciation. Many species underwent repeated episodes of geographic shifting, vicariance, and reunion of their distributions in response to the astronomical climatic oscillations, without speciation although intraspecific adaptive changes may have accumulated (Vrba 1992, 2005). For speciation to occur, physical change must be strong enough to produce population isolation, but not so severe as to result in extinction, and the isolated phase must be of sufficiently long duration for the changes which define speciation (divergence of the fertilization system) to occur. It has been suggested that most speciation requires sustained isolation or near isolation, without rapid reintegration on the Milankovitch timescale, and that shrinking populations are important in which habitat resources are dwindling and competition increases, with consequent strong selection from the changing environment (Vrba 1995b). In the absence of physical change of appropriate kind and duration, although species may accumulate new adaptations, they are buffered against speciation at several levels (review in Vrba 2005).

One prediction is that most lineage turnover, speciation and extinction, has occurred in pulses, varying from tiny to massive in scale, across disparate groups of organisms, and in predictable temporal association with changes in the physical environment (Vrba 1985b, 2005). If we think of origination, several possible patterns of origination frequency could result, all different from the temporally random pattern predicted under H_0: (1) origination could in principle be confined to rare, large pulses in response to the largest environmental changes. Such large pulses may resemble jagged mountain crests, or dissected high plateaus, rather than simple, single peaks because the timing of turnover responses to climatic or tectonic episodes will differ among organismal groups and local areas. (2) Many, frequent, small pulses, such as in response to the 100 Ka astronomical cycle, interspersed by the less frequent, larger ones described under (1). (3) Combinations of the random null model and the turnover-pulse hypothesis suggest additional predictions such as a random background of turnover frequency punctuated by rare pulses. A comparison among turnover pulses is expected to show much heterogeneity – or "mosaic" differences. The environmental changes that trigger turnover are diverse. They vary in nature, intensity, timing – how long they endure, how much fluctuation occurs, and steepness of component changes and net trends – and in geographic emphasis and extent, from very localized to present in many parts of the earth. Topographic and latitudinal factors contribute to geographic variation in the turnover responses to a major global change. Also, the different organismal groups differ sharply in how they are affected by climatic variables (see Andrews and O'Brien 2000 for mammals). They differ in response (by speciation, extinction, intraspecific evolution, or no response at all). Lineages which do undergo turnover initiated by a given physical change may do so with different timing (in "relays," see examples in Vrba 1995b, 1995c). Thus if a turnover pulse is detected in a data set, it is desirable to study subdivisions of those data to understand the detailed taxonomic, geographic, and temporal patterns.

Additional hypotheses: (1) Under habitat theory and other concepts which invoke predominant allopatric speciation, the species should generally "start small," namely, in geographic distributions that are more restricted than those they attain later on (Vrba and DeGusta 2004). H_0 does not predict this. (2) Of two areas of similar large size, both subject over the same time to climatic cyclic extremes that remain habitable for organisms; the area that is more diverse in topography will have higher incidences of selection pressures and vicariance per species. The prediction is that the topographically more diverse area has higher rates of vicariance, speciation, and extinction (Vrba 1992). (3) During periods of strong latitudinal thermal contrasts, with ice caps on one or both poles, biomes closest to the equator are predicted to have higher speciation and extinction rates than biomes at adjacent, higher latitudes (e.g., this bias may have contributed to the high species richness in the tropics today, Vrba 1985b, 1992.). (4) Biome generalists are expected to have lower rates of vicariance, speciation, and extinction than biome specialists (Vrba 1980, 1987a, 1992). Because habitat theory stresses physically initiated vicariance and selection pressure, changes in amplitude and mean of the climatic cycles, and in which cycle predominates, are expected to affect the evolutionary outcome. The larger the amplitude, the higher the incidence of vicariance and selection pressure at any cyclic extreme, accelerating the rates of intraspecific adaptation, speciation, and extinction. Changes in cyclic dominance can affect the frequency and duration of vicariance. Large translations in the climatic mean and envelope may be especially significant for speciation and extinction (Vrba 1995b: Figs. 3.2, 3.3).

The Coordinated Stasis Hypothesis

Brett and Baird's (1995) hypothesis of coordinated stasis is Darwinian in a focus on organismal interactions in a community as a source of stasis. It proposes that the coevolutionary bonds during stasis are so strong that physical change is needed to disrupt them to result in turnover. Thus this model is "community based" in its theoretical assumptions (see also the hypothesis of coevolutionary disequilibrium of Graham and Lundelius 1984 and reviews in Barnosky 2001; Vrba 2005). Brett and Baird's (1995) model predicts stasis of species, interrupted by pulses of speciation and extinction, across all communities in which a set of species occurs. Thus, their predictions are closely comparable with those of the turnover-pulse hypothesis, as acknowledged by Brett and Baird (1995:287): "The same term [coordinated stasis] could be used for the blocks of stability in Vrba's (1985b) 'stability-pulse' hypothesis."

The Variability Selection Hypothesis

This hypothesis was proposed and applied to hominin evolution by Potts (1998a, 1998b, 2012; pages quoted are from the 1998a paper unless otherwise noted). It is about (1) a particular category of adaptations which he calls "variability selection adaptations" (VSAs), (2) their initial appearance and establishment, (3) their fate in the face of long-term climatic cycles, and (4) an interpretation of the theoretical implications of their evolution:

1. VSAs are "structures and behaviors responsive to complex environmental change" (p. 81), which are uniform within species "yet able to mediate secondary phenotypic traits that vary. . ." (p. 85). His examples include a locomotor system allowing a wide repertoire of movement and "a large brain or specific neurological structure that is effective in processing external data and generating complex cognitive responses" (p. 85).
2. VSAs arise first in isolated populations. Intraspecific polymorphism results with VSAs in some populations and not in others. Organismal selection from short-term variability during organismal lifetimes initially promotes such VSAs (or at least allows them to persist).
3. The long-term evolutionary outcome at Milankovitch and longer timescales is that organisms with VSAs survive climatic extremes. Therefore species, which include at least one VSA-carrying population, survive. Over time the VSAs can become more elaborate as climatic extremes recur. Thus, high climatic amplitude at timescales longer than organismal life times, notably at Milankovitch and longer timescales, causally influences the evolutionary outcome.

4. Climatic variability at the longer timescales is a selective agent of VSAs, which are "designed [by selection] to respond to novel and unpredictable adaptive settings" (p. 85). That is, these organismal adaptations are shaped by selection for the function of flexible responses to future climatic excursions of the Milankovitch cycles, and this is a new kind of selection: "variability selection" (VS).

Potts regards his concept as distinct from previous concepts, notably from the (p. 82) "savanna hypothesis" and other "environmental hypotheses of hominin evolution [which focused] on a specific type of habitat." Proposals (1), (2), and (3) are severally and jointly consistent with previous theoretical proposals (see section "Ecological Specialists and Generalists"). The sole departure is proposal (4) of a distinct type of selection, which is commented on next.

The special effects which the high amplitude of climatic cycles since the late Pliocene had on the biota (e.g., that species, in which generalist adaptations for climatic tolerance evolved, survived disproportionately) has been much discussed (e.g., Stanley 1985; Vrba 1985a, 1992, 2000). No one doubts that strong Milankovitch excursions can selectively remove some populations and species whose organisms are unfit under those conditions, nor that generalist adaptations of survivors can sequentially be elaborated during recurrent such episodes. But this would not be a new kind of selection. *Organismal selection* cannot promote adaptations to future Milankovitch extremes, although *inter-demic selection* (Wright 1932, 1967) or *species selection* (review in Vrba 1989b) could in principle occur at those longer timescales. (In fact, Potts did at one stage wonder whether his notion might represent a form of lineage or species selection, R. Potts pers. comm.). The problem is that the concept of selection and adaptation at levels higher than that of organisms is onerous (Williams 1966; Maynard Smith 1987; Vrba and Gould 1986; Vrba 1989b). Maynard Smith (1987) discussed this as follows (p. 121): "We are asking whether there are entities other than [organisms] with the properties of multiplication, heredity, and variation, and that therefore evolve adaptations by natural selection." Considering the nature of the adaptations Potts (1998a) had in mind, one probably does not need to invoke higher level selection. Such issues on levels of selection have been extensively debated and with respect to diverse organismal case histories. An example which is of interest here, in spite of (and perhaps because of) being far removed from hominins on the tree of life, is the case in diatoms of the resting stage adaptation to polar conditions of long winter darkness (Kitchell et al. 1986): The fossil record shows that diatoms living in Arctic waters just before the Cretaceous/Tertiary (K/T) boundary already had this life cycle adaptation. Kitchell et al. (1986) documented that during the K/T mass extinction (which involved long-term global darkening), diatoms and other photosynthetic planktonic groups with resting stages had markedly lower extinction rates than groups which lacked this seasonal adaptation. They argued (correctly in my view) that these life history features, which arose by selection at the organismal level as adaptations to seasonal variability, were also fortuitously (by sheer luck) available and useful during the K/T event for weathering much longer intervals of darkness. They concluded that this sorting among species, although nonrandom, does not represent species selection but species sorting according to the effect hypothesis (Vrba 1980). The adaptation is this case could not have been selected at the organismal level for climatic variability at the timescale of mass extinction. The selective forces and character complexes which contributed to the survival of hominins and other mammals in the face of increasing climatic amplitude during the late Neogene may in principle fall into the same category.

Additional Comments on Environmental Hypotheses of Hominin Evolution

In the current spirited and exciting debate on the various hypotheses (savanna, variability selection, turnover pulse, habitat theory, and more), some confusion has crept in, which is affecting the debate in a negative way to the point where sometimes the discussants are talking past each other. While Potts (2012:154) wrote that "Regarding the external drivers of human evolution, the primary alternative to Vrba's TPH [turnover pulse hypothesis] has been the variability selection hypothesis," the points raised here are relevant to all the hypotheses and all parts of the debate. Three such issues will be mentioned here.

1. **Specific Habitats, Species-Specific Habitats, and Other Specific Notions.** Consider these quotations: "The VS [variability selection] hypothesis differs from prior views of hominin evolution, which stress the consistent selective effects associated with specific habitats or directional trends (e.g., woodland, savanna expansion, cooling)" Potts (1998a:81). "Habitat-specific adaptations may entail a more limited responsiveness to environmental perturbation..." (Potts 1998a:155). "Over the past three decades, the environmental study of human evolution has been dominated by the search for the preferred [i.e., specific] habitat of each hominin species. This approach has led to a far more static concept of early hominin adaptation..." (Potts 1998a:161). This pits "consistent selective effects," "specific habitats" and "habitat-specific adaptations" of "limited responsiveness," and directional climatic trends (the not-so-good "static concept") against variable selective effects, variable habitats, and "variability selection adaptations" and pervasive climatic oscillations and environmental complexity (the good, dynamic concept). But is this a substantive dichotomy with correct characterization of both sides? It is not, and one "culprit" is the interpretation of the word "specific."

   In the present context, "specific" simply means "relating to, characterizing, or distinguishing a species," thus neutral on breadth and changeability of adaptation, habitat, or environment in this case. The definition of the specific habitat of a species (see third paragraph in introduction of this review, which describes how many including the present author have used it) is indeed neutral on degree of variability, referring only to a list of resources and their ranges which describes where and how the species can live. In principle, the resource ranges of the specific habitat can be extremely broad. Consider an extreme and hypothetical example of a land species which can live everywhere within a temperature range of 0–100 °C. Its specific habitat with respect to temperature is the range 0–100 °C. A related point: the notion that each species is "specific for a particular *habitat*" does not equate with specificity for a particular – or single – type of *environment*. For example, the aardvark, while a specialist in terms of food and substrate, ranges widely across Africa from semidesert to dense, moist woodland. A species' habitat may remain intact although it lives in strongly fluctuating environments over long time, such as the aardvark whose habitat and resources persisted as widely varying environments swept over the areas in which it lived. In other cases, habitat variability – such as variable use of food and substrate – is an integral part of the habitat specificity of the species (see 2).

Unfortunately, such simple misunderstandings can spread and eventually harden. For example, deMenocal (2004:4) stated that "most environmental hypotheses of African faunal evolution are 'habitat-specific' (Potts 1998b) in that they consider faunal adaptations to a specific environment, most commonly the emergence of grassland savannah…"

2. **Adaptation to Variability.** Potts (1998a, 1998b, 2012) regards the VSA (variability selection adaptation) concept as distinct from previous concepts of adaptation, such as the generalist adaptations which confer eurytopy (Eldredge 1979), broad habitat specificity (Vrba 1987a), and broad climatic tolerance (Stevens 1989). He considers "habitat-specific" adaptations (e.g., Vrba 1987a) and selection pressures as different from VSAs and VS because the former in his view narrowly refer to a particular kind of environment and not to variable environments. He is wrong in these claims.

   Structures and behaviors that confer flexibility in the face of – and are usually ecophenotypic or genetically based adaptations to – climatic variations, and that may arise and exist as polymorphic variants in species, are well known (e.g., the resting/vegetative life cycle in diatoms noted above, hibernation, etc.) including complex behaviors in primates (e.g., the presence in some Japanese macaque populations of grass-washing behavior, Nakamishi et al. 1998). Concerning human evolution, as reviewed below, many have written about adaptation to variability (including environmental heterogeneity at any one time) and the effects of climatic cycles. As Potts (2012:154) considers habitat theory and the VS hypothesis as "primary alternatives," any impression that previous discussions of human evolution in the light of habitat theory (e.g., Vrba 1985a, 1989a) have ignored hominin adaptation to climatic variability needs to be corrected. One hypothesis (Vrba 1989a:30) concerns culture in general:

   > *The culture of the genus* Homo *is a generalist adaptation.* Hominine culture is an extension of the common phenomenon in other animals that use behaviour to cope with climatic conditions. … a special case among animal behaviors that confers an expanded use of environmental resources. In contrast, robust australopithecines were more specialized on open, arid habitats. . . .[and in *Homo* occurred] a switch to the crucial generalist adaptations of brain and culture that have made us the least environment-dependent species on earth today.

It turns out that Vrba's (1989a) hypothesis that the robust australopithecines "were more specialized on open, arid habitats" is probably wrong (see review below). However, it now seems likely that the masticatory features of *Paranthropus*, while adaptations for consuming tough or gritty foods, had the effect of broadening, not narrowing, the range of food items consumed and allowed these forms to subsist in varied environments (Wood and Strait 2003).

One hypothesis on hominin adaptation to climatic variability, which is plausible and deserving of testing, is that humans descend from deep nomadic (migratory) ancestry, at least since the onset of advanced bipedalism in *Homo* ca. 1.6 Ma, which falls during a time of change to more open and seasonally arid landscapes:

> As Baker (1978) observed, most animals are 'migratory' to some extent. But it is undeniable that those living in open, arid habitats, where resources tend to be patchy in space and/or time, invariably have a greater tendency to seasonal and more extensive movement... Did one or both of the hominin lineages that diverged during the Pliocene migrate seasonally across ecotonal margins? (Vrba 1985a:70).

If evidence of hominid nomadism in the Early Pleistocene were to be found (as it might be, for instance, by isotopic analysis of diet in conspecific hominins), one would still need to ask whether that nomadic potential was there previously or whether it evolved de novo by genetically based broadening of the norm of reaction to allow both nonmigratory and migratory behavior depending on seasonality. If the latter is true, then migratory behavior by *Homo* could surely be termed a good habitat-specific adaptation and a good variability selection adaptation. The use of different wording does not change the logic of that.

3. **Climatic Variability.** Potts (1998a, 1998b, 2012) concluded that others with versions of the savanna hypothesis that were articulated previous to his VS hypothesis, which includes me, were focusing narrowly on long-term cooling trends and failed to incorporate observations about patterns of African paleoclimatic variability from deep-sea cores and recently also from coring on the African continent (Scholz et al. 2007; Cohen et al. 2007; reviewed below). Again, the issue must be taken with this. First of all, the focus on long-term trends (e.g., Vrba 1995b) is a necessary part of the study of climatic variability in mammalian evolution: the shorter-period Milankovitch cycles modulate each other which gives rise to cycles of longer periods (and therefore to long-term cooling and warming trends) which are associated with ice sheet expansion and cooling and turn out to be important triggers of mammalian speciation and extinction (e.g., cycles with periods of ca. 1 Ma and ca. 2.4–2.5 Ma; see van Dam et al. 2006). More generally, it was the realization of the potentially enormous implications of the climatic oscillations for evolution of new form, function, and species in hominins and other mammals – of the fact that the "species specific for these . . . biomes are riding along on their 'habitat plates', that drift back and forth rapidly . . . over the tectonic plates that drift more slowly beneath" (Vrba 1992:11) – that prompted the organization of an interdisciplinary conference to explore those implications (Vrba et al. 1995). It was argued then

(Vrba 1995a:33) that "if prolonged vicariance is important for turnover and especially for speciation, then major shifts in the *mode*, or periodicity pattern, of the astronomical cycles should be examined for associated turnover" (see also Vrba 1992), and a model was illustrated (Vrba 1995a:30–33), using Shackleton's (1995: Fig. 17.3) data which records delta^{18}O variation at 0.003 Ma interval steps for the past 6 Ma, for measuring climatic variability. Because this way of measuring climatic variability monitors the outer envelope of climate curves step by small step, it is expected to detect major changes in climatic mode such as documented by deMenocal and Bloemendal (1995): a shift from dominant climatic influence occurring at 23–19 Ka periodicity prior to ca. 2.8 Ma to one at 41 Ka variance thereafter, with further increases in 100 Ka variance after 0.9 Ma (see also Ruddiman and Raymo 1988). (Some results will be compared in section "Physical Background: Climatic Change" with those of others who have measured variability in climatic curves, including Potts 1998a.)

In sum, how do the turnover-pulse hypothesis (within in more general habitat theory which includes responses to climatic variability of generalists and specialists) and the variability hypothesis compare in terms of content? Readers will make up their own minds. My conclusion is that they do not differ substantively in terms of the basic processes implied. There are differences in emphasis, in terms used, and in how the terms they have in common are interpreted (particularly the term "specific habitat" of species).

Is the early savanna hypothesis still alive and well? Yes, the basic hypothesis – that climatic change has caused reductions in wood: grass cover proportions which affected hominin populations and evolution – remains a good one, although it has evolved and branched out into more sophisticated versions. Cerling et al. (2011) showed that the fraction of woody cover in tropical ecosystems can be quantified using stable carbon isotopes in soils and applied the method to fossil soils from hominin sites in the Awash and Omo-Turkana basins. They concluded (p. 55) that "the combined results from two of the most significant hominid-bearing regions in eastern Africa leave the savanna hypothesis as a viable scenario for explaining the context of earliest bipedalism, as well as potentially later evolutionary innovations within the hominin clade."

Tests Based on the Temporal Distribution of Newly Appearing Phenotypes and Species

The models above all predict significant concentration in time of particular newly appearing morphologies and in the case of the coordinated stasis and turnover-pulse hypotheses also of speciation and extinction events. All of them predict that such events in the fossil record should associate significantly with climatic change. Most difficulties in testing such hypotheses have to do with errors in the chronological, physical, and biotic data and with testing at inappropriate temporal, geographic, and taxonomic scales (Barnosky 2001). There are two types of errors in such tests:

inferring fossil events that are not there (i.e., erroneous rejection of H_0, Type I error) and failure to detect real events (Type II error) as exemplified by Signor and Lipps (1982). Take, for example, a Type II error under the turnover-pulse or coordinated stasis hypotheses, the attempt to distinguish between H_0, and real small speciation pulses that occurred at the Milankovitch timescale. Such a test using first appearance data with lower time resolution (e.g., the data for 0.5 Ma-long intervals length in Vrba and DeGusta's 2004 study of African mammals) will fail, although major pulses might be detectable. The main bias that leads to Type I error, seeing pulses that are not there, arises from unequal fossil preservation between time intervals, areas, and groups of organisms, the "gap bias" (Vrba 2005): any given species' fossil FAD (first appearance datum) may postdate its true, or cladistic, FAD (Kimbel 1995). Gaps have the effect that, for instance, a count of FADs in an interval is erroneously inflated by FADs of species which in reality originated (but were not detected) previously. An early version of a test that corrects for the "gap bias," thus allowing a rigorous test of the pulse hypothesis, was applied to the African larger mammals of the past 20 Ma divided into 1 Ma-long intervals (Vrba 2000). More recently, a second, updated form was applied to the nearly 500 African species recorded over the past 10 Ma divided into 0.5 Ma-long intervals (Vrba and DeGusta 2004; Vrba 2005). Time resolution in this record is sufficiently good, with more than 70 % of the site records dated by radiometric or paleomagnetic means, that any large speciation (or extinction) pulses spaced sufficiently far apart in time should be detectable. Some results will be mentioned in section "The Record of First Appearances of Mammalian Species."

Physical Change, Adaptation, Speciation: Evidence from the African Neogene

Physical Background: Climatic Change

Following the definitive documentation of the astronomical cycles (Hays et al. 1976), it was thought that they may have had little effect on the tropics in general (review in Burckle 1995) and on African hominin-associated environments in particular. For example, Hill (1995:187) considered that "it may be that African terrestrial vertebrate habitats were to some extent buffered from climatic changes seen elsewhere." Hill's caution is well taken that specific areas may "march to a local drummer" especially if that drumbeat derives from tectogenesis (see below). It now appears that much of Africa participated in global as well as more localized climatic changes over the time period of interest, namely, the late Miocene-Recent record, as the earliest hominin fossils currently date to ca.7 Ma ago (Brunet et al. 2004). For much of this time Africa has been influenced by two separate processes (deMenocal 2011): forcing from the orbital precession cycle has brought about monsoonal cycles that alternated between wet and dry conditions, and superimposed on these was a long-term trend toward increasingly more arid and more variable conditions.

The Late Miocene. Changes in polar ice volume and sea level have greatly influenced African climate and human evolution as cited variously below. By the time hominins evolved, there had been large ice sheets in Antarctica since 33 Ma (following a previous time of ephemeral ice sheets), while the earliest extensive Arctic glaciation was established much later, by 2.7 Ma and contemporaneously with the first appearance of *Paranthropus*, the robust australopithecines, and probably also of the lineage to modern humans. Miller et al. (2005) discussed the relations of ice sheets, global climate, and sea level and considered that sea level mirrors oxygen isotope variations, reflecting ice-volume change and thus global climate on the 10,000 year–1,000,000 year timescale which applies to human evolution. They found prominent sea level falls and thus global climatic events, at 8.2 Ma, 5.7 Ma, 4.9 Ma, 4.0 Ma, 3.3 Ma, and 2.5 Ma. There was ice buildup on West Antarctica and general increase in delta^{18}O values 7.0–5.0 Ma ago (Kennett 1995). A major cooling which started before 6 Ma and peaked shortly thereafter contributed to isolation and desiccation of the Mediterranean Basin during the Messinian low-sea level event and salinity crisis dated ca. 5.8–5.3 Ma (Haq et al. 1980; Hodell et al. 1994; Bernor and Lipscomb 1995; Aifa et al. 2003; Garcia et al. 2004). This major cooling coincides with a strong vegetation change ca. 6.3–6 Ma, with a large decrease in tree cover and increased aridity in both West and East Africa, according to Bonnefille's (2010) overview of macrobotanical (fossil wood, leaves, and fruits) and microbotanical (mainly pollen) evidence for the past 10 Ma in tropical Africa with special reference to the hominin sites. After the Messinian followed warming and a transgressive phase started before 5 Ma and reached a maximum in the 5–4 Ma interval, according to Haq et al. (1987).

Questions remain on the African effects of these late Miocene climatic events. Kingston et al. (1994) found that, in the Kenyan Tugen Hills area, a heterogeneous environment with a mix of C_3 and C_4 plants – and without grassland dominance – persisted over the entire past 15 Ma without any apparent local influence from global climatic change. Yet evidence from Lothagam indicates that this part of Kenya experienced strong environmental changes over the latest Miocene (Leakey et al. 1996; Leakey and Harris 2003). Further evidence comes from analyses of carbon isotope ratios in soils and fossil tooth enamel. Cerling et al. (1997) studied fossil herbivores ranging over the past 22 Ma from several continents. Using the fact that low delta^{13}C values in herbivore teeth reflect a diet of mainly C_3 plants, while high values indicate feeding on C_4 plants, they found that up to 8 Ma ago, mammals in Pakistan, Africa, and South and North America had C_3 diets or C_3-dominated diets. By the late to latest Miocene, C_4 plants came to dominate the diets. In Kenya, representing the lowest latitude in the sample, the transition was complete by between 8 and 6.5 Ma and in Pakistan by ca. 5 Ma. Cerling et al. (1997) interpreted their results as showing a global increase in the biomass of C_4 plants 8–6 Ma ago which resulted from a decrease in atmospheric CO_2.

The Plio-Pleistocene. Interest in African hominin-associated climatic changes has burgeoned greatly over the past decade. Here, only a few examples are given from the large volume of evidence for the Plio-Pleistocene, from research on broader regional climatic variability, to illustrate some of the basic lines of enquiry and the diversity of approaches. Additional evidence more directly focused on hominin environments will follow below. Clemens et al. (1996) discussed how monsoon variability and evolution respond to external forcing (orbitally driven changes in solar radiation) and internal forcing (interaction among the atmosphere, oceans, land surface, and ice sheets). They examined a deep-sea sediment record spanning the past 3.5 Ma from the northwest Arabian Sea and compared diverse proxies, including abundances of *Globigerina bulloides*, biogenic opal content which indicates radiolaria and diatom production, and lithogenic grain size of the deep-sea sediments, all of which in this area can indicate the strength of the Asian monsoon. Clemens et al. (1996) argued that the growth of Northern Hemisphere ice sheets over the past 3.5 Ma weakened the Asian summer monsoon and increased the aridity of subtropical Asia and eastern Africa. They demonstrated that the phase relationships between the African monsoon and the glacial cycles were shifting continuously over the past 2.6 Ma, explaining why indicators of surface water such as lake levels and of vegetation, such as dust spikes, often do not covary. The authors found significant shifts in the intensity and phase of the Indian monsoon at ca. 2.6 Ma, 1.7 Ma, 1.2 Ma, and 0.6 Ma. deMenocal (2008, 2011:541) discussed the large amplitude of the African wet-dry monsoon cycles using the example of changes in the Sahara and pointed out the usefulness of sapropel layers as proxies (see also Rossignol-Strick 1985; Rossignol-Strick et al. 1998) for detecting the intensity and phase of the monsoon cycles:

> From 15,000 to 5,000 years ago, the modern Saharan Desert was nearly completely vegetated, with large, permanent lakes and abundant fauna. Precessional increases in summer radiation invigorated the monsoon, delivering more rainfall deeper into Africa, and enhanced Nile river runoff flooded into the eastern Mediterranean Sea. The resulting freshwater stratification created anoxic conditions and led to deposition of organic-rich sediments (sapropels) on the seafloor.

Similarly, Cole et al. (2009, 2012) found evidence for the prevalence of extensive paleolakes in the Sahara during the African humid period.

The opposite extreme, “megadrought,” has also been documented. In companion papers, Scholz et al. (2007) and Cohen et al. (2007) presented results from drill cores from Lake Malawi and point out that by 2007, these were the first long and continuous, high-fidelity records of tropical climate change from the African continent itself. Their record documents periods of severe aridity between 135 Ka and 75 Ka ago, when the lake’s water volume was reduced by at least 95 %. Scholz et al. (2007:16416) wrote, “Surprisingly, these intervals of pronounced tropical African aridity in the early late-Pleistocene were much more severe than the Last Glacial Maximum, the period previously recognized as one of the most arid of the Quaternary.” According to Cohen et al. (2007:16422), “Fossil and sedimentological data show that Lake Malawi itself, currently 706 m deep, was reduced to a ca. 125 m deep saline, alkaline, well mixed lake.”

Among Plio-Pleistocene records that demonstrate the large effects of global climatic change on Africa, many are based on signatures from plants, algae, or other indicators of overall plant cover such as dust. Pollen cores off West Africa record the shifting of the Sahara-Sahel boundary and the earliest extensive spread of the Sahara desert ca. 2.8–2.7 Ma ago (Dupont and Leroy 1995). One of the two strongest vegetation changes found by Bonnefille (2010) across tropical Africa over the past 10 Ma occurred at 2.7 Ma (p. 391): "abrupt decline of forest pollen accompanied by an increase in grass pollen was found at 2.7 Ma, . . . accompanied by a significant increase in C-4 grass proportions, well indicated in the Turkana region and likely explained by an increase in dry season length." Marlow et al. (2000) used an index based on the ratio of two types of alkenones (chemical compounds produced by specific species of haptophyte algae) to measure sea surface temperature (SST) in a marine core off Namibia. They presented their continuous time series of changing SST for the past 4.5 Ma, as well as estimates of paleoproductivity from the mass accumulation rates of organic carbon, diatom abundances, and diatom assemblages. Marlow et al. (2000) interpreted decreased upwelling to represent warmer conditions with wetter, more mesic periods in southern Africa and concluded that SSTs decreased markedly, in association with intensified Benguela upwelling, after 3.2 Ma, with subsequent periods of marked SST decrease and upwelling intensification near 2.0 Ma and 0.6 Ma. Another marine record from southwestern Africa, off Angola, derived from carbon isotope analyses of wind-transported terrigenous plant waxes, indicated African C_4 plant abundances 1.2–0.45 Ma (Schefuss et al. 2003). The evidence showed that the African vegetation changes are linked to SST in the tropical Atlantic Ocean and that changes in atmospheric moisture content due to tropical SST changes and the strength of the African monsoon controlled African aridity and vegetation changes. Marine records off West Africa and from the Gulf of Aden have documented delta^{18}O variations and also dust influxes from the Sahara and Sahel regions in the West and from Arabian and northeastern African areas in the Gulf of Aden (deMenocal and Bloemendal 1995; deMenocal 2004). The latter paper reported steplike shifts in the amplitude and period of eolian variability at 2.8 (±0.2) Ma, 1.7 (±0.1) Ma, and 1.0 (±0.2) Ma.

As one method to use climatic records to predict over which time intervals vicariance (population fragmentation) should be particularly concentrated, the following hypothesis was introduced with discussion on how to test it: "*long-term, continuous vicariance*, and long-term increases and decreases in the minimum- and maximum-value envelopes of the astronomical climatic cycles, are the kinds of allopatry and climatic change that are particularly important for speciation" (Vrba 1995b:27 and following pages). Shackleton's (1995: Fig. 17.3) data were used, which record delta^{18}O variation at 0.003 Ma interval steps for the past 6 Ma, to identify periods over which the largest net cooling or warming trends occurred. (Vrba 2004: take an interval t_x of length x Ka, for example, t_{100} for $x = 100$ Ka, and move it step by step along the time axis from early to late. At each interval step, mark the interval along the time axis if either of conditions C, for cooling, or W, for warming, is true. C: the upper [warm] envelope of the climatic curve remained continuously below the running mean of the previous 300 Ka, i.e., the interval is a $t_{100,C}$, or an interval of length 100 Ka with marked cooling. W is the corresponding condition for a warming trend. A pattern of $t_{100,C}$ and $t_{100,W}$ distribution in time results, with data clusters for the most sustained trends. I here report results for separate assessments using interval lengths in Ka of x = 40, 65, 100, and 140.) The following approximate intervals (in chronological sequence) emerged as times of sustained net cooling ($t_{40,C}$, $t_{65,C}$, $t_{100,C}$, and $t_{140,C}$ are respectively labelled as *, **, ***, and ****, from least to most severe; time ranges in ca. Ma): 6–5.7****, 5.1–4.9*, 4.2–3.9*, 3.4–3.2***, 2.9–2.3 especially 2.7–2.5****, 2.1–2.0*, 1.8–1.65**, 0.95–0.85**, and 0.8–0.65** (and 0.8–0.6*). Intervals of net warming (similar notation as for cooling): 5.6–5.35****, 4.5–4.4*, 3.1–2.9*, 1.65–1.6*, and 0.85*. Because this method of measuring changes in climatic variability, in this case in delta^{18}O variability, monitors the outer envelope step by small step, it is expected to detect major changes in climatic mode such as documented by deMenocal and Bloemendal (1995): a shift from dominant climatic influence occurring at 23–19 Ka periodicity prior to ca. 2.8 Ma to one at 41 Ka variance thereafter, with further increases in 100 Ka variance after 0.9 Ma (see also Ruddiman and Raymo 1988). Comparison with the results in the previous paragraph shows that this way of measuring change does succeed in detecting the major dominance shifts. There are now several such approaches. For example, Potts (1998a) subtracted the lowest from highest value for each unit million year as a measure of total climatic variability for that unit year. He found that variation of 0.3–0.5 parts per million (ppm) is obtained for most of the Neogene until the 6.0–5.0 Ma interval, during which variability rose sharply. After a minor decrease during 5 to 4 Ma, there were increases during every succeeding interval with the highest one, to 1.9 ppm, during the past 1 Ma (Potts 1998a:83, Fig. 1). Donges et al. (2011) applied a nonlinear method of time series analysis, recurrence network, to records of dust flux. They found (p. 20422) three “transitions between qualitatively different types of environmental variability in North and East Africa during the (i) Middle Pliocene (3.35–3.15 Ma B. P.), (ii) Early Pleistocene (2.25–1.6 Ma B. P.), and (iii) Middle Pleistocene (1.1–0.7 Ma B. P.),” which approximately also appear among my results, as does the mode change 6.0–5.0 Ma ago found by Potts (1998a).

It is worth noting the major climatic changes, including some with rough consensus on when they occurred, from the diverse sources cited above: 8.2 Ma, 7–6 Ma, and associated with the Messinian ca. 5.8–5.3 Ma, ca. 5 Ma, 4.2–3.9 Ma, 3.5–3.2 Ma, 2.9–2.3 Ma, 1.8–1.6 Ma, 1.2 Ma, and 1.0–0.6 Ma.

Physical Background: Tectonism

Tectogenesis has featured less prominently than climate change in discussions of evolution, perhaps because it is mostly a slow process and the date limits for events tend to be wide. Yet it has had a primary influence on landscape and biotic evolution. This includes hominin evolution especially in rift-associated environments as recognized long ago by Coppens (1988–1989). Crustal changes influenced climate on a grand scale, e.g., the late Pliocene closure of the Isthmus of Panama may have led to the start of the modern ice age (Maier-Reimer et al. 1990; Haug et al. 2001). The uplift of western North America, the Himalayas, and the Tibetan

Plateau possibly influenced the Pleistocene cooling intensification ca. 1 Ma ago (Ruddiman et al. 1986). Northward drift of Africa during the Neogene led to southward displacement and areal decrease of tropical African forests and contributed to long-term aridification (Brown 1995). Episodes of intensified African uplift since ca. 30 Ma ago, which raised the entire eastern surface higher than in the West, greatly affected the African climate (Burke 1996). Apart from the numerous localized climatic effects of tectogenesis (e.g., Feibel 1997), the *topographic diversity* it generates *together with the superimposed climatic cycles* constitutes a prime cause of spatial and temporal environmental heterogeneity, changing selection pressures, and speciation (Vrba 1992). Thus evolution of the African Rift had an especial role in some evolutionary events in hominins (Coppens 1988–1989) and other mammals (e.g., Denys et al. 1987). The present episode of rifting began in the Early Miocene (Frostick et al. 1986). Ca. 8–6 Ma ago, a general increase in African tectonic activity led to formation of the Western Rift (Ebinger 1989). A major episode of uplift coincided with the climatic changes ca. 2.5 Ma ago (Partridge and Maud 1987). After 6 Ma ago, the rift system continued to propagate to the southwest toward the Kalahari Craton (Summerfield 1996). One incipient zone of rifting, trending southwest from Lake Tanganyika, terminates in central Botswana, where faulting and tilting of the zonal margins have resulted in damming of the Okavango River to spread out as the extensive inland Okavango Delta (Scholz et al. 1976).

I suggest that the dynamics of the hydrological features associated with rifting – rivers redirected, lakes forming and disappearing, and especially the inland deltas spreading at the margins of incipient rift zones – have had a particular impact on the evolution of hominins and other biota. All early hominins required permanent water, and many of the eastern African hominin sequences reflect riverine and rift margin associated deltaic and lake environments (e.g., Harris et al. 1988; Brown and Feibel 1991). The significance of inland deltas is that they can form vicariated "islands" of mesic conditions – or refugia – throughout periods of aridification and even in the absence of topographic heterogeneity. The edges of such a refugium are ecologically heterogeneous with intrusions of the arid surrounding environment. ("Refugium" here means a biome refugium, e.g., a forest refugium preserves the characteristic forest vegetation physiognomy, although its detailed taxonomic composition may differ from that of the parent forest community.) The Okavango Delta provides a good example: it is a vicariant island – despite the very low relief of the area (Scholz et al. 1976) – of woodland savanna and water almost entirely surrounded by semidesert. Many of the hominin-bearing strata represent times when the areas were such inland deltaic-riverine-lacustrine refugia (Vrba 1988). This poses problems for our ability to recognize times of widespread climatic change across the larger areas because "climatic change in the larger region is recorded in a refugium only close to its ecotonal limits, by the new appearances (or disappearances) of peripheral taxa . . . that represent occasional intrusive elements from the alternative biome" (p. 410). An important implication from the evolutionary perspective is this: as climatic changes were sweeping across much of Africa at the Milankovitch scale, such inland deltas were recurrently isolated and reconnected as parts of larger continuous biomes. During the reconnected phases, migration and gene flow occurred. During the vicariant phases, there was enhanced incidence of gene pool divergence among populations, selection pressures at the refugial margins, intraspecific phenotypic diversification, and speciation. If it is true that inland deltas can in this way act as centers of phenotypic diversity and speciation and that they are particularly prevalent at the tilting margins of incipient rift zones, this would predict a late Neogene propagation of centers of increased speciation in a South-southwesterly direction as the rift evolved.

The Record of First Appearances of Mammalian Species

All Larger Mammals. As noted above, a method which corrects for the "gap bias" was applied to the African larger mammal record of the past 10 Ma. Such correction is especially important in the late Neogene climatic context because open, mesic to arid areas tend to preserve vertebrate fossils better than do the more forested, wetter ones (Hare 1980). The following results emerged (largely agreeing with those in Vrba 1995c, 2000, in so far as they are comparable): over the past 8 Ma, the strongest turnover pulses, involving both origination and extinction, occurred in the 5.5–5.0 Ma and 3.0–2.5 Ma intervals. (The dating of the earlier pulse is tentative as there are no physical dates, and this event may belong to the 6.0–5.5 Ma interval; I will refer to the 5.5 Ma event.) Each of the intervals 7–6.5 Ma and 3.5–3.0 Ma had an origination pulse without an extinction pulse and 1.0–0.5 Ma ago an extinction pulse without an origination pulse. Where one can compare this set of turnover events with the strongest cooling trends, the coincidence in time and intensity is strikingly close: the strongest climatic event, cooling toward ~2.5 Ma ago, coincides with the strongest turnover pulse, while lesser cooling and turnover events are present in the intervals 3.5–3.0 Ma and 1.0–0.5 Ma. The results also showed intervals of significantly low origination and extinction, some of which overlapped with periods of high sea level with low polar ice on a warmer earth (Haq et al. 1987; Hodell and Warnke 1991).

The African mammalian record and the bias-correction model which was used continue to be updated. The results do give preliminary support to the hypothesis that at least a substantial part of turnover in African mammals was initiated by climatic change and that global cooling with increased aridity and increased seasonality was a more important stimulus of turnover than was global warming (Vrba 2000, 2005). Of the cooling trends, the one toward 2.5 Ma was the strongest, followed by a lesser trend starting ca. 1 Ma ago. Yet individual glacial maxima became colder after 2.5 Ma, especially after 1 Ma (Shackleton 1995). The fact that there were no further major origination pulses after 2.5 Ma suggests that most of the lineages present then were either species that had evolved during the start of the modern ice age with adaptations to the new environments or long-lasting biome generalists that survived right through that cooling trend.

A related result is that of Vrba and DeGusta (2004). We studied the question of whether most species "start small," namely, in geographic distributions that are more restricted than those they attain later on. We used the same 10 Ma-long record of the African larger mammals and the correction for the "gap bias." The number of fossil site records from which each species is known in an interval was taken as a proxy for the magnitude of its living geographic range and abundance in that interval. We then tested H_0 that the geographic spread of species remained averagely constant across successive survivorship categories, namely, from the first appearance (FAD) interval to the immediately following one, and so on. We found that the mean number of site records increased strongly from the FAD interval to the following survivorship interval, followed by a less marked although still significant increase to the next interval, with no significant changes thereafter. Thus we concluded that the average large African mammal species has indeed started its life in a relatively small population and thereafter increased in geographic range to reach its long-term equilibrium abundance by ca. 1 Ma after origin. This supports hypotheses of speciation that accord a major role to the formation of isolated populations of reduced size initiated by physical change.

Not everyone has agreed that global change was a driver of evolutionary change and speciation in African hominins and other mammals. For instance, one aim of Behrensmeyer et al. (1997) was to test Vrba's (1995c) finding of a turnover pulse in African mammals between ca. 2.8 and 2.5 Ma by examining the past 4.5 Ma in the Turkana Basin (including the northern Shungura Formation, Ethiopia, and the southwestern Nachukui and southeastern Koobi Fora Formations in Kenya). They concluded that there was "no major turnover event between 3.0 and 2.5 Ma" (p. 1591) and that this "weakens the case for rapid climatic forcing of continent-scale … faunal turnover" (p. 1593). I have reservations about their methods and assumptions which differed substantially from mine (Vrba 2005). A reexamination of Turkana Basin evolution over 4.0–1.0 Ma divided into 0.5 Ma-long intervals, using my African mammal database and the statistical "gap bias" model outlined above, showed a single significant origination pulse in the 3.0–2.5 Ma interval and no extinction pulses (Vrba 2005). Separate examination of the northern and two southern areas of the Turkana Basin indicated a strong speciation (and extinction) pulse in the North 3.0–2.5 Ma ago, but none in the combined or separate southern areas. This result is consistent with the southward spread of the Sahara Desert in the latest Pliocene (Dupont and Leroy 1995), which affected the northern basin more strongly, eliciting significant turnover, while the southern deltaic-lacustrine areas may have behaved more nearly like biome refugia. More recently, Bobé and Behrensmeyer (2004:399) found that between 4 and 1 Ma in the Turkana Basin, "episodes of relatively high faunal turnover occurred in the intervals 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma. *Paranthropus* and *Homo* appear in the Turkana Basin during successive intervals of high turnover at 2.8–2.6 and at 2.4–2.2 Ma, while the appearance of *Homo erectus* is coupled to a major episode of turnover and grassland expansion after 2 Ma." (See also Bobé's 2011, comprehensive overview.)

At least some studies show that the larger mammalian turnover pattern is also reflected in small mammals. Among micromammals of the Shungura Formation, Ethiopia (Wesselman 1995), at 2.9 Ma woodland taxa predominated and even rainforest taxa were present (e.g., the bush baby *Galago demidovii*, a rainforest species today). These forms were displaced by new grassland-to-semidesert species by 2.4 Ma. The turnover includes terminal extinctions, immigrants from Eurasia such as a hare, *Lepus*, and global first appearances of species, such as a new species of *Heterocephalus*, the genus of desert-adapted naked mole rats, and a new species of the ground squirrel genus *Xerus* (Wesselman 1995). This time also marks the first African and global debuts in the record of several species of bipedal, steppe-, and desert-adapted rodents, such as the genus *Jaculus* of desert gerboas (Wesselman 1995) and a new springhare species, *Pedetes*, in South Africa.

Evidence for turnover pulses has by now been found in many records from different continents and time intervals and in diverse taxa, from marine invertebrates (e.g., Lieberman 1999) to mammals in areas beyond Africa (e.g., Azanza et al. 2000; Raia et al. 2005; van Dam et al. 2006). The last study, of a dense, long (24.5–2.5 Ma) record of rodent lineages from Spain, adds an intriguing element. It showed the existence of turnover cycles with periods of 2.4–2.5 and 1.0 Ma, which van Dam et al. (2006) linked to low-frequency modulations of Milankovitch oscillations. Specifically, the pulses of turnover occur at minima of the 2.37 Ma eccentricity cycle and nodes of the 1.2 Ma yr obliquity cycle. Obliquity nodes and eccentricity minima are associated with ice sheet expansion and cooling and affect regional precipitation. As the average duration of African larger mammal species over the past 20 Ma is close to the period of the eccentricity cycle (2.33 Ma, Vrba and DeGusta 2004), the question arises: did a substantial proportion of those species originate at one eccentricity minimum, and become extinct at the next, and could hominins have been a part of that?

The Hominin Record. The hominid sample is too small (15 to more than 20 species depending on which sources are consulted) to test whether most hominin species "started small" and to test for turnover pulses using the statistical methods which were applied to all larger mammals. Nevertheless it is of interest to compare the known hominin FAD record with the timing of major climatic trends and speciation pulses in all larger African mammals. The earliest appearance of hominins, *Sahelanthropus* from Chad (Brunet et al. 2004), is ca. 7.2–6.8 Ma according to Lebatard et al. (2008). The hominin clade originated 8–5 Ma ago based on molecular estimates (Ruvolo 1997). Thus, the first appearance of hominins in the record participates in the elevated mammalian origination toward 6.5 Ma ago, in an interval marked by increased African tectonic activity (Ebinger 1989), and ice buildup in West Antarctica with global cooling (Kennett 1995). The FAD of *Orrorin tugenensis* ca. 6 Ma (Senut et al. 2001; Sawada et al. 2002) occurs near the end of the strong and widespread decrease in tree cover and increased aridity over ca. 6.3 and 6 Ma reported by Bonnefille's (2010). The genus *Ardipithecus* from the Middle Awash area, Ethiopia, includes two species to date: *A. kadabba* from the western margin in 5.7–5.2 Ma-old strata (Haile-Selassie 2001; Haile-Selassie et al. 2009) and *A. ramidus* dated 4.4–4.2 Ma at Aramis (White et al. 1994; WoldeGabriel et al. 1994; White, Asfaw et al. 2009) and with a similar date at Gona Western Margin (bracketed 4.51–4.32 Ma, Semaw et al. 2005). Thus, the FAD of *Ardipithecus* is associated temporally (and possibly also causally) with the major climatic changes which accompanied the Messinian ca. 5.8–5.3 Ma ago and with the ca. 5.5 Ma turnover event in African mammals.

Most African FADs of hominin species are mid-Pliocene to mid-Pleistocene in age, during which time the intervals of strongest climatic change were (see review above) 4.2–3.9 Ma, 3.5–3.2 Ma, 2.9–2.3 Ma, 1.8–1.6 Ma, 1.2 Ma, and 1.0–0.6 Ma and possibly also near 2 Ma and 4 Ma. Together, these episodes occupy ca. 40 % of the past 5 Ma. Yet most, and possibly all, of the hominin FADs either coincide with or fall very close to one of these events (chronology mostly after Wood and Richmond 2000; Wood and Leakey 2011): *Australopithecus anamensis* first appears at ca. 4.2 Ma and *A. afarensis* ca. 4.0 Ma (3.8 Ma or possibly 4 Ma according to Wood and Leakey 2011); FADs of *A. bahrelghazali*, *Kenyanthropus platyops* and possibly also *A. africanus* are a part of the mammalian origination pulse in the 3.5–3.0 Ma interval which may be a response to the cooling trend ca. 3.5–3.2 Ma; *Australopithecus garhi*, *Paranthropus aethiopicus*, *P. boisei*, and possibly also *Homo habilis* and *H. rudolfensis* have FADs in the 2.8–2.3 Ma interval. The FADs of *Australopithecus sediba* (Berger et al. 2010; Pickering et al. 2011), *H. ergaster*, and *H. erectus* (and its migration to Eurasia) between 2.0 and 1.8 Ma may also be associated with major climatic change. While taphonomic factors and chance may have contributed to this pattern, it does leave intact the hypothesis of climatic cause of at least most hominin speciation. An important splitting event in the hominin clade was the one that led to *Paranthropus* on the one hand and *Homo* on the other. Several systematic studies have concluded that the characters of *A. afarensis* are consistent with it being the common ancestor of *Paranthropus* and *Homo* and possibly also of one or more additional lineages (e.g., Kimbel 1995; Asfaw et al. 1999). After enduring in apparent equilibrium since ca. 4 Ma, *A. afarensis* is last recorded just after 3.0 Ma (Kimbel et al. 1994), while its descendants appear variously between 2.7 Ma and 2.3 Ma. Kimbel (1995:435) concluded: “regardless of which phylogenetic hypothesis is more accurate, it is clear that a pulse of speciation occurred in the hominin lineage between 3.0 and ca. 2.7 Ma, producing at least three lineages.” The phylogenetic pattern, of an inferred ancestor ending after 2.9, with new descendants branching off between 2.9 and 2.3 Ma ago, is common in bovids (e.g., Vrba 1995c, 1998a). These concordant genealogical patterns among different mammalian groups strongly suggest the causal influence of the start of the modern ice age, namely, that common causal rules connect the climate system with evolution of different biotic groups. It remains to be seen whether additional information in the future will support these preliminary indications that major changes in the mode of the climatic pattern and the concomitant changes in African environments were important causal influences on speciation in hominins, just as they were in many other mammalian lineages.

Climate in Relation to Habitats and Adaptations of Hominins

Bonnefille’s (2010) review of African vegetational evolution provides a particularly good context for this section because of its broad temporal and geographic scope, which encompasses the Cenozoic with focus on the past 10 Ma, includes the recent vegetation, and ranges right across the African tropics with emphasis on areas and sites which have yielded hominins. She discussed both the macrobotanical and the microbotanical evidence and its relationship to results from recent isotopic studies and from Atlantic and Indian Ocean deep-sea cores. Her conclusions include the following (Bonnefille 2010:409):

> the palaeontological hominid record so far documented appears embedded within a long evolution of tropical vegetation bracketed between two main events. These two events are the most pronounced among all of the many that occurred during the last 10 Ma. They had the strongest impact on past vegetation, at the continental scale, both in west central and eastern Africa..... The first event was a strong shift from an important forest expansion (7.5–7 Ma) to an abrupt retreat with minimum tree proportion (6.5–6 Ma) concerning the whole tropical region, half a million years before the Messinian salinity crisis. . . . The second event (2.7–2.5 Ma) was the arid shift, from forest to savanna expansion, corresponding to maximum expansion of the northern hemisphere glaciation. . . . [It involved] greater and more widespread aridity, increase in C_4 grass abundance in lowlands savanna and steppe, and the relative expansions of mountain forests coincide with the appearance of the genus *Homo* and stone tools registered simultaneously at different sites in East Africa.

Her summation stresses how pervasive mixed vegetation types are in tropical Africa, namely, areas which include both wooded and open habitat in close geographic proximity (p. 409): "*Mixed tree and grass cover* are among the widely spread vegetation conditions [and have] *persisted throughout the last 10 Ma*."

I have added the italic emphasis in the last sentence because it reflects a convergent theme in early hominin environmental research over the past decade, as apparent in the following discussion of the hominin species in terms of their natural surroundings, adaptations, and habits: the vegetational and other local conditions surrounding each of the early hominin species were heterogeneous and mosaic.

The earliest known hominins (or presumed members of the hominin clade; not all agree) are *Sahelanthropus tchadensis* (Brunet et al. 2002), ca. 7 Ma old, and *Orrorin tugenensis* (Senut et al. 2001) from Lukeino, Kenya, ca. 6–5.7 Ma (Sawada et al. 2002). The associated fauna of *Sahelanthropus* according to Brunet et al. (2005:753) "indicates a mosaic of landscapes probably resembling that of the present-day Okavango Delta (Botswana)." The Okavango Delta today "is an interlocking mosaic of habitat types" (Paterson 1976:55). These range from permanent swamp, wetlands, and seasonally inundated open areas, through higher-lying grasslands, dry scrub, woodland, to very dense woodland with high and nearly closed tree canopy and water margin forest, and many of the mammal species are virtually confined to particular parts of this mosaic (Ramberg et al. 2006).

The environment of *Orrorin* was initially described as follows by Senut (2006:89): "It has been widely accepted that hominins (and thus bipedalism) emerged in a savannah environment. However, it is now clear that the earliest bipeds are associated with forested environments as proved by the flora and the fauna of the Lukeino Formation (Kenya, 6 Ma)." But detailed studies of the mammals indicated a more heterogeneous environment (Mein and Pickford's 2006:183 micromammal study):

> The presence of galagids, fruit bats and the diversity of dendromurines (3 species) and some probably arboreal murids (possibly ancestral to *Thallomys* or *Grammomys*) indicates the presence of trees in the vicinity of the site, but some of the taxa suggest the presence of

> relatively open environments in the vicinity of Kapsomin at the time of deposition. A similar mixture of vegetation types is indicated by the large mammals from Lukeino.

Bonnefille (2010) linked the strong decrease in tree cover in both East and West Africa after 7 Ma to the earliest hominins as follows (p. 390):

> At that time, very arid conditions shown by scarce tree cover occurred over the whole tropical region. … Generally arid conditions coincide with the accepted timing for the chimpanzee/hominid split, and record of *Sahelanthropus tchadensis* in Chad and *Orrorin tugenensis* in Kenya, although these fossils were found under locally wooded environment.

This underlines the important point that patterns and causal actions at different hierarchical levels should not be conflated, because they are to some extent decoupled and relate only indirectly and in subtle ways: at the more inclusive climatic level "very arid conditions" and "scarce tree cover [spread] over the whole tropical region," just as at the higher phylogenetic level of species, there were changes in population structure toward vicariance that in some cases resulted in speciation and extinction. At the more local scale were those "habitat islands," each with its "interlocking mosaic of habitat types," in Paterson's (1976) words, and buffered to some extent from the larger geographic pattern of aridity and low wood cover, with the hominins and other organisms adapting to those local conditions. We still know very little about what the earliest hominids were doing. Bipedal locomotion of some kind has been claimed for both *Sahelanthropus* (Brunet et al. 2002) and *Orrorin* (Pickford et al. 2002), although doubts on that have been expressed, for example, by Harcourt-Smith and Aiello (2004), who considered that the earliest evidence for bipedalism is only arguably from *Sahelanthropus*, *Orrorin*, and the next taxon discussed here, *Ardipithecus*.

Ever since the announcement of *Ardipithecus ramidus* as a candidate for the "long-sought potential root species for the Hominidae" (White et al. 1994:306, who described it as *Australopithecus ramidus*), there has been a debate about its morphology, phylogenetic position, and its habitat 4.4 Ma ago at the source site Aramis. Some of the unexpected and astonishing features and implications of this taxon, especially after subsequent discovery that more than 110 additional specimens from 4.4 Ma stratum include a partial skeleton with much of the skull, hands, feet, limbs, and pelvis, are reflected by the following statements by White, Asfaw et al. (2009:75):

> This hominid combined arboreal palmigrade clambering and careful climbing with a form of terrestrial bipedality more primitive than that of *Australopithecus*. *Ar. ramidus* had a reduced canine/premolar complex and a little-derived cranial morphology and consumed a predominantly C_3 plant-based diet (plants using the C_3 photosynthetic pathway). Its ecological habitat appears to have been largely woodland-focused. *Ar. ramidus* lacks any characters typical of suspension, vertical climbing, or knuckle-walking. *Ar. ramidus* indicates that despite the genetic similarities of living humans and chimpanzees, the ancestor we last shared probably differed substantially from any extant African ape. Hominins and extant African apes have each become highly specialized through very different evolutionary pathways.

Concerning the Aramis habitat, White, Ambrose et al. (2009) wrote (p. 87):

> Assessment of dental mesowear, microwear, and stable isotopes from these and a wider range of abundant associated larger mammals indicates that the local habitat at Aramis was

> predominantly woodland. The *Ar. ramidus* enamel isotope values indicate a minimal C_4 vegetation component in its diet (plants using the C_4 photosynthetic pathway), which is consistent with predominantly forest/woodland feeding. Although the Early Pliocene Afar included a range of environments, and the local environment at Aramis and its vicinity ranged from forests to wooded grasslands, the integration of available physical and biological evidence establishes *Ar. ramidus* as a denizen of the closed habitats along this continuum.

In their response to White, Ambrose et al. (2009) and also to companion papers by WoldeGabriel et al. (2009) and Louchart et al. (2009), Cerling et al. (2010) disagreed and stated that from their analysis of the stable isotopic record (p. 1105d): "we find the environmental context of *Ar. ramidus* at Aramis to be represented by what is commonly referred to as tree-or bush-savanna, with 25 % or less woody canopy cover," and that "although we do not judge the validity of the savanna hypothesis, we note that from the stable isotopic record, the connection between bipedalism and C_4 grass expansion starting in the late Miocene and continuing into the Pliocene remains a viable idea." White et al. (2010) replied that Cerling et al.'s (2010) reconstruction of a predominantly open grassland environment with riparian woodland is inconsistent with a wealth of fossil, geological, and geochemical evidence. While they acknowledged that the local environment in the vicinity of Aramis ranged from dense woodland/forest to wooded grassland, White et al. (2010:1105) held firm that "in the Middle Awash, *Ar. ramidus* fossils are confined to the western portion of the sampled Pliocene landscape where the species is associated with woodland to grassy woodland habitat indicators." More recently, Cerling et al. (2011) investigated the percentages of woody cover, using stable carbon isotopes, in fossil soils from hominin sites in the Awash and Omo-Turkana basins. They concluded (p. 55) that "the combined results from two of the most significant hominid-bearing regions in eastern Africa leave the savanna hypothesis as a viable scenario for explaining the context of earliest bipedalism, as well as potentially later evolutionary innovations within the hominin clade."

As coauthors of White, Ambrose et al. (2009), David DeGusta and I contributed inference of the paleohabitat based on bovid astragali (DeGusta and Vrba 2003), especially of the overwhelmingly most common species which is a tragelaphine antelope, namely, that 4 Ma ago in Aramis, *A. ramidus* lived in (or at least spent a lot of time in) a woodland habitat. Additional inferences from the bovids suggest that there were wetlands and water bodies nearby (thus, Louchart et al.'s 2009:66e1, conclusion that the woodlands were "distant from large water bodies" is not one I share) and that there were also grassland areas in the vicinity. Namely, the notion that the Aramis environment was a mosaic of habitats among which *A. ramidus* preferred the dense woodlands seemed (and still seems) reasonable to me. I wonder whether we may find future support for the hypothesis that, since ape ancestry, *Ardipithecus* had already diverged toward a measure of broader use of environmental resources and the more generalized ability to live within a vegetationally mosaic environment. The results of Levin et al. (2008) give encouragement to consider this possibility seriously. They concluded (Levin et al. 2008:215) that

> the spectra of isotopic results from herbivores found in late Miocene *Ar. kadabba* and early Pliocene *Ar. ramidus* sites at Gona are most similar to isotopic values from extant herbivores living in bushland and grassland regions and dissimilar to those from herbivores living in closed-canopy forests, montane forests, and high-elevation grasslands. The tooth enamel isotopic data from fossil herbivores make it clear that *Ardipithecus* at Gona lived among a guild of animals whose diet was dominated by C_4 grass, and where there is no record of closed-canopy vegetation.

However, the notion that *A. ramidus* at Aramis was tied to – or at least strongly preferred – woodlands (albeit situated in a mosaic of habitats) seems to be compatible with what Semaw et al. (2005:301) reported for *Ardipithecus ramidus* from As Duma, Gona, Ethiopia, that "the Early Pliocene As Duma sediments sample a moderate rainfall woodland and woodland/grassland."

Kimbel et al. (2006) argued persuasively that *A. anamensis* and *A. afarensis* represent parts of an anagenetically evolving lineage or evolutionary species. In Bonnefille's (2010) broad overview of the large-scale African changes which led to the origin and establishment of this lineage, she noted that the period from 6 to 4 Ma was marked by a progressive increase in tree cover that culminated at 3.9 Ma, during *A. anamensis* time and before the first appearance of *A. afarensis*. From their stable isotope-based diet reconstructions of Turkana Basin hominins, Cerling et al. (2013:10501) concluded that "*Australopithecus anamensis* derived nearly all of its diet from C_3 resources . . . [while] by ca. 3.3 Ma, the later *Kenyanthropus platyops* had a very wide dietary range-from virtually a purely C_3 resource-based diet to one dominated by C_4 resources."

Bedaso et al. (2013) used carbon and oxygen isotopes of mammalian tooth enamel to reconstruct paleoenvironments of *A. afarensis* from the Basal Member (ca. 3.8–3.42 Ma) and the Sidi Hakoma Member (3.42–3.24 Ma) of the Hadar Formation in the Middle Pliocene locality of Dikika, Ethiopia. Their results indicate a wide range of foraging strategies, characterized by mixed C_3/C_4 to C_4-dominated diets in wooded grasslands to open woodlands and that (2013)

> the middle Pliocene habitat structure at Dikika could be as diverse as open grassland and wooded grassland, and woodland to forest in the Sidi Hakoma Member while wooded grassland, woodland to grassland are evident in the Basal Member. All habitats except closed woodland and forest are persistent through both members; however, the relative proportion of individual habitats changed through time. . . . Thus, the existence of *A. afarensis* throughout the middle Pliocene indicates either this species might have adapted to a wide range of habitats, or its preferred habitat was not affected by the observed environmental changes.

Kingston and Harrison (2006) used similar methods and reached similar conclusions on a heterogeneous environment for *A. afarensis* from the Laetoli Beds in Tanzania, much further south. While over the long term many African records show that cooling was accompanied by aridification, it is by no means an invariable association, as expected from the shifting phase relationship between the monsoon and glacial cycles. For example, pollen data from Hadar, Ethiopia, show that "*Australopithecus afarensis* accommodated to substantial environmental variability between 3.4 and 2.9 Ma ago. A large biome shift, up to 5 °C cooling, and a 200- to

300-mm/year rainfall increase occurred just before 3.3 Ma ago, which is consistent with a global marine delta^{18}O isotopic shift" (Bonnefille et al. 2004:12125).

Wood and Richmond (2000) considered the tibia of *Australopithecus anamensis* (ca. 4.2 Ma; Leakey et al. 1995) the earliest undisputed evidence of bipedalism and in thinking about the ecology of the *anamensis-afarensis* lineage, recall the debate on selective factors which might have promoted the inception and advancement of bipedalism. Much new evidence now clearly indicates that the relevant lineages since the late Miocene were probably all living in patchy environments, mosaics of habitat types, with patches of dense woodland and forest, light woodland, grassland, and interrupted by barriers such as volcanic deposits and watered areas including seasonally flooded wetlands. Selection pressure for traversing the barriers to reach resources on the other side (which may have been what the *A. afarensis* individuals who formed the Laetoli footprints were doing; Leakey and Hay 1979), or for foraging in these areas (as in a shallow delta or wetland) might have promoted the onset or, later on, elaboration of bipedality. The notion that wading in shallow water played a part (Niemitz 2000; Verhaegen et al. 2002) seems reasonable given what we know about the palaeoenvironments of many early hominid species. In such a mosaic context some additional previous hypotheses of what caused the adoption of upright posture may apply: carrying, display or warning, new feeding adaptations, control of body temperature, tools, and stone throwing. Reviews are given by McHenry (1982), who thought that hominin bipedalism "could have arisen as an energetically efficient mode of terrestrial locomotion for a small_bodied hominoid moving between arboreal feeding sites" (p. 163), and by Preuschoft (2004).

Whatever the combination of selective forces, there is much healthy debate on how the postcranial anatomy of early hominins should be interpreted in terms of function, habitat use, and phylogenetic relationships. Harcourt-Smith and Aiello (2004)) reviewed some of the evidence (including the Laetoli footprints, the AL 288-1 *A. afarensis* skeleton, postcranial material from Koobi Fora, the Nariokotome *H. ergaster* skeleton, "Little Foot" [StW 573] from Sterkfontein, South Africa, fossils of *Orrorin*, *Ardipithecus*, and *Sahelanthropus*) and pointed out the greater diversity in bipedalism (or putative bipedalism) in earlier hominins than previously suspected. In each of their three phylogenetic scenarios (Harcourt-Smith and Aiello 2004: Fig. 4), the postcranial diversification coincides broadly with the 3.0–2.3 Ma period of the largest Pliocene climatic trend. More recently, Haile-Selassie et al. (2012) reported a new hominin foot from a new site Woranso-Mille in the central Afar, Ethiopia, which further increases the diversity of Pliocene bipedal adaptations. They wrote (p. 565):

> Here we show that new pedal elements, dated to about 3.4 Ma ago, belong to a species that does not match the contemporaneous *Australopithecus afarensis* in its morphology and inferred locomotor adaptations, but instead are more similar to the earlier *Ardipithecus ramidus* in possessing an opposable great toe. This not only indicates the presence of more than one hominin species at the beginning of the Late Pliocene of eastern Africa, but also indicates the persistence of a species with *Ar. ramidus*-like locomotor adaptation into the Late Pliocene.

There has also been input from South Africa into the debate on diversity and environmental associations of hominin locomotion. Clarke and Tobias (1995) proposed that the foot bones from Sterkfontein Member 2 (StW 573, Little Foot, dated ca. 4 Ma, Partridge et al. 2003, see below) reflect a foot that had not sacrificed arboreal competence or hallucial opposability and that this suggests dense tree cover in the environment. Based on fossil pollen, it has been suggested that the preferred habitat of *A. africanus* at Makapansgat was subtropical forest and that selective pressures associated with densely vegetated environments played a role in the evolution of bipedalism (Cadman and Rayner 1989; Rayner et al. 1993). Potts (1998a) dubbed this the "forest hypothesis" of bipedal origin. The fossil bovids associated with *A. africanus* at Makapansgat and Sterkfontein do not suggest a uniform forest, although a mosaic in the greater area which includes dense and open woodland patches, as well as grassy patches and permanent water, could be consistent (Vrba 1974, 1980, 1987b), which agrees with Reed's (1997) conclusions. A related insight comes from Lee-Thorp et al.'s (2010) analysis of stable isotopes in the tooth enamel of more than 40 hominin specimens, including *A. africanus* from Makapansgat and Sterkfontein and *Paranthropus robustus* from Swartkrans and Kromdraai together spanning ca. 3–1.5 Ma. They concluded (p. 3389) that among all these South African australopithecines including *A. africanus* and persisting over the entire time range, "these data demonstrate significant contributions to the diet of carbon originally fixed by C_4 photosynthesis, consisting of C_4 tropical/savannah grasses and certain sedges, and/or animals eating C_4 foods. Moreover, high-resolution analysis of tooth enamel reveals strong intra-tooth variability in many cases, suggesting seasonal-scale dietary shifts." (See also Sponheimer et al. 2013.) These results suggest spatial variability in vegetation cover and also seasonal variability, rather than predominant forest.

Australopithecus afarensis, which persisted in place through major climatic and vegetational variability (e.g., at Hadar, Bonnefille et al. 2004; Bedaso et al. 2013), appears to have been the most generalist of all hominin species up to the Middle Pliocene. It was geographically so widespread that in the past one wondered why it was not also found among the South African hominins. The findings of Partridge et al. (2003) suggested that the *anamensis-afarensis* lineage may well have been present there as well: based on cosmogenic aluminum-26 and beryllium-10 burial dates of low-lying fossiliferous breccia in the Sterkfontein caves, associated hominin fossils such as skeleton StW 573 date to ca. 4 Ma, the time of the *anamensis-afarensis* transition in East Africa.

An important splitting event in the hominin clade was the one that led to *Paranthropus* on the one hand and *Homo* on the other. Several systematic studies have concluded that the characters of *A. afarensis* are consistent with it being the common ancestor of *Paranthropus* and *Homo* and possibly also of one or more additional lineages (e.g., Kimbel 1995; Asfaw et al. 1999). After enduring in apparent equilibrium since ca. 4 Ma, *A. afarensis* is last recorded just after 3.0 Ma (Kimbel et al. 1994), while its descendants appear variously between 2.7 Ma and 2.3 Ma. Kimbel (1995:435) concluded that "regardless of which phylogenetic hypothesis is more accurate, it is clear that a pulse of speciation occurred in the hominin lineage between 3.0 and ca. 2.7 Ma, producing at least three lineages." The phylogenetic pattern, of an inferred ancestor ending after 3.0 Ma, with new descendants branching off between that and 2.3 Ma ago, is common in bovids (e.g., Vrba 1995c, 1998a).

According to Wood (1995), the first signs of the "hypermasticatory trend" occurred with an advent of *Paranthropus aethiopicus* ca. 2.6 Ma ago, followed by exaggeration in this trend ca. 2.3 Ma with the FAD of *P. boisei*, and further lesser modifications to the dentition of this species between 1.9 and 1.7 Ma. Efforts to find out what the robust australopithecines were eating, and where they lived, have been ongoing for a long time. A study which uses functional morphology of mammalian assemblages associated with early hominins to reconstruct their environs by Reed (1997) is particularly useful because it treats the East and South African Plio-Pleistocene fossil assemblages in the same analysis, comparing them with each other and with extant mammalian communities from different habitat types. Reed (1997) concluded that *Paranthropus* species in East and South Africa lived in both wooded and more open environments, always in habitats that include wetlands. This is compatible with our earlier findings for the relevant South African sites, based on bovid abundances (Vrba 1975) and also on the assemblages as a whole (Brain 1981b), which indicated environs of *P. robustus* including substantial grassland with wooded patches and permanent water indicated by water-dependent fauna.

The notion that robust australopithecines, *Paranthropus*, were in certain senses specialists was originally proposed by Robinson (1963) based on the dentition of *P. robustus*. He suggested that the "crushing, grinding" robust vegetarian specialist lived in a somewhat wetter and more luxuriant environment than did the earlier gracile omnivore *A. africanus*. Prompted by the bovid evidence of change to more open vegetation in the *Paranthropus*- and *Homo*-bearing strata, compared to the earlier South African ones with only *A. africanus*, the question arose whether the musculature of *P. robustus* was massive and the molars proportionally so large "because their 'vegetables' were of the tough grassland type" (Vrba 1975:302) and whether, in contrast to the more generalized *Homo*, robust australopithecines may have been more specialized on open and relatively more arid habitats. Based on comparisons of the dental microwear of *A. africanus* and *P. robustus*, Grine (1981, 1986) concluded that the latter had probably processed tougher food items. Wood and Strait (2003) did a thorough analysis of the proposal that *Paranthropus* species were feeding specialists. They concluded that *Paranthropus* species were most likely ecological generalists (i.e., eurybiomic in being able to make a living in varied environments) and made the novel proposal that (p. 149) "… although the masticatory features of *Paranthropus* are most likely adaptations for consuming hard or gritty foods, they had the effect of broadening, not narrowing, the range of food items consumed." I accepted their arguments because the acquisition, in response to newly encountered environments, of morphology which can perform a new specialized function but which at the same time permits the retention of functions evolved in the ancestral more uniform environment, is a recurrent theme in the evolution of generalist mammals (e.g., the impala *Aepyceros melampus* which, from a browsing ancestry, Vrba and Schaller 2000, evolved cranial and dental features which allow mastication of grass and other tough plant matter and also a stomach structure which undergoes reversible seasonal changes, Hofmann 1973, a rare adaptation to varied vegetational environments. As a consequence of these dental and digestive evolutionary advances, the impala is today a consummate herbivore generalist which can subsist in different environments by switching its dietary intake).

A number of isotopic analyses of diet and environment have since contributed to illuminating such questions. van der Merwe et al. (2008) did isotopic dietary studies of *H. habilis* and *P. boisei* teeth from Olduvai, Tanzania, and discussed how the results compare with previous ones for the South African hominins (see citation of Lee-Thorp et al. 2010, above). They found that the two Olduvai species had very different diets, while, in contrast, the isotopic analyses of the three South African species of early hominins, *A. africanus*, *P. robustus*, and *Homo* sp., showed considerable variation in individual diets but no marked differences between species. For two Olduvai specimens of *P. boisei*, van der Merwe et al. (2008) found C_4 dietary components (77 % and 81 %) that far exceeded those of the South African taxa, including *P. robustus*, and indeed of all other early hominins for which carbon isotope values were available by that time. They pointed out that the C_4 input could come from consuming grasses, some sedges and forbs, and a variety of animals which eat C_4 plants and suggested that *P. boisei* may have fed on papyrus or other C_4 species of Cyperaceae which are perennially available near water. A similar study by Cerling et al. (2013) on hominins in the Turkana Basin showed comparable results: by ca. 2 Ma, specimens attributable to the genus *Homo* provide evidence for a diet with a ca. 65/35 ratio of C_3- to C_4-based resources, whereas *P. boisei* had a higher fraction of C_4-based diet (ca. 25/75 ratio). Thereafter *Homo* sp. increased the fraction of C_4-based resources in the diet through ca. 1.5 Ma, whereas *P. boisei* maintained its high dependency on C_4-derived resources. Sponheimer et al. (2013:10513) summarized their overview of isotopic evidence of early hominin diet as follows:

> Before 4 Ma, hominins had diets that were dominated by C_3 resources and were, in that sense, similar to extant chimpanzees. By about 3.5 Ma, multiple hominin taxa began incorporating ^{13}C-enriched [C_4 or crassulacean acid metabolism (CAM)] foods in their diets and had highly variable carbon isotope compositions which are atypical for African mammals. By about 2.5 Ma, *Paranthropus* in eastern Africa diverged toward C_4/CAM specialization and occupied an isotopic niche unknown in catarrhine primates, except in the fossil relations of grass-eating geladas (*Theropithecus gelada*). At the same time, other taxa (e. g., *Australopithecus africanus*) continued to have highly mixed and varied C_4 diets.

Together all the available lines of evidence for species of *Paranthropus* support a degree of generalism in terms of the patchiness, from open to more wooded, of vegetational environments they inhabited and dietary specialization in the east African species yet not in the southern *P. robustus* which evidently maintained a more mixed diet in terms of the range of C_3- to C_4-based resources. All these leave intact the possibility raised by Wood and Strait (2003) that the evolution of the masticatory features of *Paranthropus*, while allowing consumption of hard or gritty foods, may have broadened their options in the soft-to-hard-and-gritty spectrum of foods, perhaps remaining within the C_4/CAM range of plants in the case of *P. boisei* while ranging across both C_3 and C_4 resources in the case of the southern *P. robustus*.

There are two species with first appearances after the last record of *A. afarensis* which have been assigned to *Australopithecus*. The specific name *Australopithecus garhi* reflects well the reactions of many ("garhi" means "surprise" in the Afar language) when they found out about the mosaic combination of its anatomical features relative to previously known hominins and the tantalizing associated evidence of cultural advances (which may or may not be the handiwork of this species), all at the hitherto under-represented age of 2.5 Ma (Asfaw et al. 1999; de Heinzelin et al. 1999). The cranial and dental remains, from the Hata beds, Bouri Formation, of Ethiopia's Middle Awash, led Asfaw et al. to conclude that (p. 629) *A. garhi* "is descended from *Australopithecus afarensis* and is a candidate ancestor for early *Homo*. Contemporary postcranial remains feature a derived humanlike humeral/femoral ratio and an apelike upper arm-to-lower arm ratio." The abundant vertebrate remains together with the sedimentology indicate an environment (de Heinzelin et al. 1999:626) that was "primarily lake marginal. Alcelaphine bovids are abundant and diverse. All indicators point to a broad featureless margin of a freshwater lake. Minor changes in lake level, which were brought about by fluctuating water input, would probably have maintained broad grassy plains leading to the water's edge." With *A. garhi* are found some of the earliest made stone tools with earliest evidence of the their use to butcher large mammals (p. 625):

> Spatially associated zooarchaeological remains show that hominins acquired meat and marrow by 2.5 Ma ago and that they are the near contemporary of Oldowan artifacts at nearby Gona. The combined evidence suggests that behavioral changes associated with Lithic technology and enhanced carnivory may have been coincident with the emergence of the *Homo* clade from *Australopithecus afarensis* in eastern Africa.

One of the specimens on which unambiguous cutmarks are visible, perhaps made during tongue removal, was identifiable to a new genus and species of a medium-sized bovid (of body size comparable to living hartebeests) in the tribe Alcelaphini, a tribe and bovid size class which are very abundant not only in this Hata Member but also were appearing in greater numbers than before all over Africa near 2.5 Ma. Looking at this earliest evidence of cutmarks made by hominins, in its faunal and environmental context, prompts one to think about the arguments of Owen-Smith (2013) who contrasted the Pleistocene large herbivore faunas of the southern continents and argued (p. 1215) that it was the African "abundance and diversity of medium-sized grazing ruminants unrivalled elsewhere ... that facilitated the adaptive transition by early hominins from plant-gatherers to meat-scavengers."

Only a few years ago, another new species of hominin was announced, *Australopithecus sediba*, based on two partial skeletons dated 2.0 Ma (by uranium-lead dating combined with paleomagnetic and stratigraphic analysis) from cave deposits at the Malapa site in South Africa (Berger et al. 2010; Dirks et al. 2010; Pickering et al. 2011). Berger et al. (2010:195) argue that *A. sediba* "is probably descended from *Australopithecus africanus*. Combined craniodental and postcranial evidence demonstrates that this new species shares more derived features with early *Homo* than any other australopith species and thus might help reveal the ancestor of that genus." The faunal fossils associated with *A. sediba* are as yet few, but consistent in chronological and environmental implications with what was found at the other hominin-associated sites thought to date near 2 Ma in the Sterkfontein area.

Near the end of the large late Pliocene cooling trend, by ca. 2.6–2.5 Ma, stone tools appeared in several other places (e.g., Semaw et al. 1997) besides the finds from Bouri, together with evidence of butchery already mentioned (de Heinzelin et al. 1999). Hatley and Kappelman (1980) proposed that the climatic change led to this behavioral advance. They showed that a high belowground plant biomass is characteristic of xeric open areas and argued that digging out of such foods, first by hand and later by digging sticks and other tools, evolved as an important feeding strategy of early hominins when the African savanna became more open and arid. Leakey (1971) noted early on that the onset of more expanded tool kits appears to overlap with the climatic change ca. 1.8–1.6 Ma ago. Another milestone dating to this time was proposed by Wood and Richmond (2000): the fact that the mandible and postcanine tooth crowns of *H. ergaster* (dated ca. 1.9–1.5 Ma) when scaled to body mass are no larger than those of modern humans may reflect the earliest cooking.

The late Pliocene and Pleistocene behavioral and cultural advances presumably reflect reorganization and expansion of the brain. The available evidence indicates significant increase in EQ (encephalization quotient) in *Homo* only over the past 2 Ma, with the largest EQ increase occurring ca. 600–150 Ka ago, according to Holloway (1970, 1972, 1978) and McHenry (1982). Shultz et al. (2012) found punctuated changes in encephalization at approximately 1.8 Ma, 1 Ma, and 100 Ka, noting that brain size change at ca. 100 Ka is coincident with demographic change and the appearance of fully modern language. Holloway et al. (2003) presented evidence that brain reorganization predated brain expansion in hominin evolution. I previously suggested that the encephalization trend in *Homo* "evolved by progressive prolongation of ancestral, fast, early brain growth phases. It started with the modern ice age, and was fuelled by progressive intensification of cooling minima since then" (Vrba 1996:15). I suspect that we may find future indications that some of the brain modifications which came to characterize *Homo* – perhaps not increase in EQ but brain reorganization – were promoted by the start of the modern ice age, which would be consistent with the proliferation of stone tool finds in the record by 2.6–2.5 Ma.

If the largest EQ increase did occur ca. 600–150 Ka ago (as cited above), it could be related to the end of the mid-Pleistocene strong climatic events ca. 1.0–0.6 Ma ago. Many selective scenarios for encephalization in *Homo* have been proposed. Falk's (1980) review included warfare, language, tools and labor, hunting, and heat stress. Gabow (1977) emphasized population structure and culture, McHenry (1982) language, and Brain (2001) our predatory past. Vrba (1985a, 1988, 1989a) proposed that major selection pressures that led to brain and cultural evolution derived from the large-scale changes in climatic mean and amplitude during the Plio-Pleistocene and that culture and the underlying brain modifications in *Homo* represent adaptation to eurybiomy or "generalist adaptation. Hominine culture is an extension of the common phenomenon in other animals that use behaviour to cope with climatic conditions . . . a special case among animal behaviors that confers an expanded use of environmental resources" (Vrba 1989a:30). As cited above, Potts (1998a) made a similar proposal to explain the brain and behavioral adaptations of *Homo*. Others have also argued that *Homo* evolved toward biome generalization (e.g., Wood and Strait 2003).

Morphological evidence of a commitment to long-range bipedalism (e.g., long legs, large femoral head) appeared much later, ca. 1.6 Ma, in the postcranial skeleton KNM-WT 15000 from Nariokotome, West Turkana (Brown et al. 1985, who assigned it to *H. erectus*; Wood and Richmond 2000 included it in *H. ergaster*). There is some agreement that the onset of advanced bipedalism in *Homo* ca. 1.6 Ma ago not only falls during a time of change to more open and seasonally arid landscapes (and near the advent of other novelties in hominin evolution, as noted above) but also makes sense as a selective response to these changes. Potts (1998a) pointed out that the latest Pliocene populations of *Homo* were increasingly mobile, for example, tool-making behavior involved long-distance transport of stones as far as 10 km. Increased mobility is reflected by the migration out of Africa by 1.8 Ma of a lineage of *Homo* (if the early date for *H. erectus* in Java, Indonesia, is correct, Swisher et al. 1994), the first of many subsequent migrations out of Africa which were associated with physical changes (Stringer 1995; Tattersall 1997b; Klein and Edgar 2002; see also Abbate and Sagri 2012, who found that the early to Middle Pleistocene *Homo* dispersals from Africa to Eurasia were temporally arranged into cycles of four major exodus waves (2.0–1.6 Ma, 1.4–1.2 Ma, 1.0–0.8 Ma, and 0.6–0.1 Ma) controlled by climatic and environmental changes).

Climate in Relation to the Evolution of Ontogeny

Heterochrony Pulses: Parallel Developmental Responses to Common Environmental Causes

The term heterochrony has been applied to both ecophenotypic and evolutionary changes in the rates and timing of ontogenetic events (Gould 1977). The same kind of heterochronic phenotype, *H*, commonly appears independently in different parts of a given monophyletic group in association with the same kind of environmental condition, *E*, and variously as an ecophenotype (i.e., reversible in later generations not faced by *E*) or as a phenotype, the expression of which is genetically fixed (or at least more constrained under varying conditions). An example is relative reduction of limb length in colder environments, an aspect of Allen's Rule (Allen 1877: mammalian extremities are reduced relative to body size in cooler climates). Not only the environmental association with *E* but also the growth patterns tend to be similar between the independent occurrences of such a phenotype *H* in a clade (e.g., Gould 1977a; Wake and Larson 1987; Vrba 1998b). It appears that certain kinds of heterochrony are more likely than others under particular environmental changes. Each heterochrony response starts off from the ancestral ontogenetic trajectory for that character, and this inheritance imparts limits and direction on what can grow and evolve. To the extent that aspects of ontogeny are shared by common inheritance between related species and across larger taxonomic groups, similar kinds of heterochrony will evolve independently in related lineages faced by the same environmental change. A summary and extension of the above is given in the following two statements (Vrba 2004, 2005):

1. Similar environmental changes elicit similar heterochronies in parallel, potentially in numerous lineages across large phylogenetic groups. Such heterochrony often involves change in body size and may be accompanied by large-scale phenotypic reorganization (Arnold et al. 1989; Vrba 1998b), such that the parallel heterochronies involve concerted evolution of suites of linked characters and "shuffling" among body proportions.
2. At times of widespread climatic change, diverse lineages may show parallel changes in size and in similar kinds of heterochrony associated in time and consistently with the climatic change – a "heterochrony pulse." "Pulse" here does not imply that the lineages responded in unison in a short time, but only that the events are significantly concentrated in time.

I will mention one particular category of heterochrony, which is associated with body size increase by prolongation of growth and which is a common mammalian response to colder temperatures. It is of special interest in the Plio-Pleistocene context of net global cooling, and it appears to have affected many African mammals including some evolutionary changes in *Homo*.

Cooling and Body Size Increase. Many species with FADs during times of cooling and aridification were larger than their ancestral phenotypes (as cladistically inferred). For example, Vrba (2004) tested H_0 that size changes across lineages are randomly distributed in time in the Alcelaphini (wildebeests, etc.) and Reduncini (waterbuck, etc.), which together comprise 63 recorded species over the past 5 Ma with a body weight range of ca. 20–250 kg. The result of significant peaks in size increase 3.0–2.5 Ma and 1.0–0.5 Ma ago, two periods with strong cooling, is consistent with Bergmann's Rule (1846: larger bodies are associated with colder temperature). While exceptions have been noted, in general, the predictions are upheld in living mammals (Ashton et al. 2000; Meiri and Dayan 2003) including in humans (Baker 1988) and in fossil mammals (Davis 1981; Kurten 1959; Heintz and Garutt 1965). To evaluate the claim that climate-associated heterochrony can involve extensive rearrangement – or "shuffling" – among body proportions, with parallel changes across related lineages, consider the example of Bergmann's Rule. Bodies can become enlarged by faster growth relative to the plesiomorphic (or directly ancestral) ontogeny, by prolongation of growth time, or by a combination of both, and the influential factors may include temperature change itself or one of the attendant environmental changes (such as seasonal changes in food and water availability, e.g., Guthrie 1984; Barnosky 1986). Such changes in growth mode are expected to result in rearrangement of body proportions. This is especially true of growth prolongation which is prevalent among Bergmann cases for which there are growth studies. For instance, many African tropical ungulates have shorter growth periods to smaller size in warm lowlands, while their close relatives at higher altitudes and/or latitudes grow for longer and become larger. The example of polymorphism in the African buffalo was noted earlier: *Syncerus caffer caffer* is much larger (up to 810 kg), grows for longer, and lives at higher latitudes and/or altitudes always near grassland, while the smaller and plesiomorphic phenotype *S. c. nanus* (up to 320 kg) with a shorter growth period lives in warmer, more forested regions.

Body Size Increase and "Shuffling" Among Body Proportions. Consider what is expected under the simplest way in which growth prolongation could occur: namely, if all ancestral growth phases for a character become proportionally prolonged (or extended in time by a constant factor) while maintaining the ancestral number of growth phases and the ancestral growth rates for respective phases (Vrba 1998b: Fig. 1). Let us call that simple proportional growth prolongation. Characters in the same organism have differing growth profiles, in terms of growth timing and rate in relation to age and body weight (e.g., Falkner and Tanner 1986), and character growth typically occurs in distinct phases in each of which character change is nonlinear with respect to age (Koops 1986). We can distinguish two major types of heterochrony and associated allometric growth under growth prolongation: (A) in type A heterochrony, characters which grow with net negative allometry with respect to age and body size will become reduced relative to body size in the adult stage of the prolonged descendant ontogeny (even if no other growth parameter changes) and paedomorphic in that the descendant adult resembles the ancestral juvenile. A probable example is the character evolution by Allen's Rule (Vrba 1998b, 2004) which is upheld in modern humans (Baker 1988). The persistence of Allen's Rule in modern biology supports the general hypothesis of similar changes in body proportions across lineages, which share inherited developmental responses to common environmental causes. (B) In type B heterochrony, characters which grow with net positive allometry become relatively enlarged. This mode, particularly by prolongation of a positively allometric late growth phase, may be how the hypermorphosed antlers of the giant Irish elk evolved (Gould 1974) and how exaggerated secondary sexual characters in enlarged bodies commonly evolve (Vrba 1998b). As growth trajectories become prolonged, some characters become relatively reduced and others enlarged, with potentially extensive rearrangement among body proportions and substantial evolutionary novelty (Vrba 1998b: Fig. 1). Type B heterochrony can also result from prolongation of positively allometric *early* growth, in which case the descendant structure is relatively enlarged and paedomorphic. An example is provided by the enlarged hind-feet of the bipedal, saltatory rodents during times of cooling (section "Climate in Relation to Habitats and Adaptations of Hominins"). If the growth of rodents, the juveniles of which in general have relatively large hind-feet

(Hafner and Hafner 1988), is prolonged, a descendant adult with enlarged hind-feet is predicted. Evidence for at least some taxa is consistent with this; e.g., bipedal Kangaroo rats, *Dipodomys*, which inhabit semiarid to arid regions in North America, have longer growth periods and are hypermorphosed in some characters – yet paedomorphosed in others – relative to the ancestral ontogeny (Hafner and Hafner 1988). As noted earlier, the bipedal forms share suites of characters in a characteristic body plan that is today strongly associated with open, arid habitats and has appeared independently in 24 genera in 8 families (Hafner and Hafner 1988). I do not know how many of the 24 instances of parallel evolution involved growth prolongation. But I suggest that at least some of these appearances of suites of integrated character complexes exemplify coordinated morphological changes, by growth prolongation, within and between lineages in response to a common climatic cause. This case illustrates that evolution by growth prolongation, as it acts on characters with different nonlinear growth profiles in the same body plan, can result in a "shuffling" of body proportions. Substantial novelty in form can result and also in function as in these rodents which can jump to a height that is from 4 to 25 times their body length. I next discuss another example of type B heterochrony with prolongation of positively allometric early growth, namely, encephalization.

Heterochrony and Brain Evolution. I applied statistical models for multiphasic growth to data on living human and common chimpanzee brain weights at ages since conception to test the hypothesis that encephalization of the human brain occurred by simple proportional growth prolongation (Vrba 1998b). Specifically, I wanted to know whether prolongation of the fetal growth phases, with strongly positive allometric growth, could account for most of the observed EQ increase. The results supported the hypothesis and imply that gross brain weight increase toward humans required change in only one growth parameter: prolongation of the nonlinear ancestral growth phases. In mammals, in general, simple growth prolongation is predicted to result in encephalization, as all mammalian brains complete a large proportion of their total growth rapidly early in ontogeny (Count 1947; Holt et al. 1975). A positive correlation of EQ with more open, seasonally cooler and drier environments has been noted in diverse mammals (Vrba 2004; e.g., in living African bovids this association is supported by comparison of the habitat preferences of the species with Oboussier's 1979 results for their EQ variation). This raises the hypothesis that there were past "encephalization pulses," across many mammalian lineages, in response to cooling over particular intervals (Vrba 1998b).

Conclusion

Environmental stimuli have influenced the evolution of hominins and other mammals at the levels of ontogeny, organismal adaptation, and speciation. From a time a few decades ago, when any proposal that climatic change is causally linked to speciation of hominins and other mammals was subjected to much doubt and even derision, there is now substantial convergence of opinion that such a linkage is real.

The climatic influence on hominin adaptation has received most attention, and some agreement has also emerged in this area: successive cooling trends since the late Pliocene were associated with the earliest evidence of – and probably initiated – the "hypermasticatory trend" in *Paranthropus* (ca. 2.6 Ma) and its later exaggeration ca 2.3 Ma, stone tools and their use to butcher carcasses (ca. 2.6–2.5 Ma), the Early Pleistocene expansion of tool kits, increased mobility by the Plio-Pleistocene interface and commitment to long-range bipedalism (ca. 1.6 Ma) in *Homo*, and significant brain expansion near 2 Ma and also since 600 Ka ago. There is some consensus that encephalization and culture in *Homo* represent generalist adaptations which conferred a more flexible and expanded use of resources (Vrba 1985a, 1988, 1989a; Potts 1998a; Wood and Strait 2003). It now seems likely that the masticatory features of *Paranthropus*, while adaptations for consuming tough or gritty foods, had the effect of broadening, not narrowing, the range of food items consumed and allowed these forms to subsist in varied environments (Wood and Strait 2003). There is less agreement on environmental stimuli of the onset of bipedalism, particularly on whether the vegetational habitats of the earliest bipedal hominins were forest to dense woodland or more open. I discussed why, even if the hominin ancestor and its bipedal descendant species both live(d) in forest, this does not necessarily mean that climatic change did not bring about speciation.

Far less work has been done on the issue of environmental causes of hominin speciation. A brief summary of the current status is as follows: in terms of theory, the expectation that allopatric speciation predominates, particularly in hominins and other large mammals, is consistent with the weight of available evidence. It would take special pleading to argue that hominins are exceptions. If allopatric speciation predominates, then so must physical initiation of speciation predominate. Most, and possibly all, of the hominin FADs either coincide with or fall very close to one of the major cooling trends. While taphonomic factors and chance may have contributed to this pattern, it does leave intact the hypothesis of climatic cause of hominin speciation. Also, on cladistic grounds, some speciation events must be closely associated with climatic change in hominins (Kimbel 1995) and other African mammals (Vrba 1995c).

Environmental stimuli of ontogenetic evolution have hardly been studied in our field. I discussed the "heterochrony pulse hypothesis": the generative properties shared among lineages can result not only in coherence of morphological changes but also in a strongly nonrandom timing of heterochrony events, as diverse lineages respond in parallel by similar kinds of heterochrony to the same environmental changes. This has not yet been tested. Of particular interest in the present Late Neogene climatic context is heterochrony involving body enlargement by prolongation of growth, because it is associated with colder (at least seasonally colder) temperatures (Bergmann's Rule, upheld in modern humans, Baker 1988). I have discussed some examples, including encephalization as a result of growth prolongation, in hominins and other mammals, and suggested that there were past "encephalization pulses," across many mammalian lineages, in response to cooling trends over particular intervals, such as during the onset and later intensification of the modern ice age.

In our field, one sometimes regrets (at least I do) that conclusive answers, such as those that emerge from some experiments of physical scientists, are so difficult to achieve. Hypotheses on the subject of environmental causes of hominin and other biotic evolution are difficult to test because the data come from different subdisciplines, each with its own set of biases, errors, and ambiguities. As a result, debates tend to continue interminably. While we have a long way to go, on the positive side, we can take heart in the simple fact that we are, so to speak, in a "growth industry": while many aspects of life are deteriorating, the fossil record with its associated geological information is constantly improving. Thus, there is an excellent expectation of decisive future progress on some of the unresolved issues. In my view, the results to date already offer support for the notion that common rules give qualitative and temporal coherence to the evolutionary responses across many mammalian – including hominin – lineages. These common rules arise from the regularities of physical change and from attributes of organismal ontogenies and phenotypes and species that are widely shared by common inheritance. The evidence implies closer linkages between the physical and biotic dynamics on earth than has traditionally been acknowledged. This perspective contrasts with the neoDarwinian view that selection of small-step random mutations is the vastly predominant evolutionary cause, with the implication that each evolutionary advance is to a larger extent an independent piece of history. Evolution is more rule bound than that, and our evolution is no exception.

Cross-References

- ▶ Contribution of Stable Light Isotopes to Paleoenvironmental Reconstruction
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Patterns of Diversification and Extinction
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of the Hominid Brain
- ▶ The Ontogeny-Phylogeny Nexus in a Nutshell: Implications for Primatology and Paleoanthropology
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ The Species and Diversity of Australopiths

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Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins

Bogusław Pawłowski and Wioletta Nowaczewska

Contents

Abstract

One of the biggest mysteries of human evolution is the divergence of the hominin lineage from the other hominoids. This chapter addresses the problem of the selective forces that might have been behind hominin emergence and that shaped this evolutionary lineage in its early stages. To establish the selection pressures that led to hominin emergence, the following issues will be discussed: (1) The time when the human–chimpanzee split could have taken place according to paleoanthropological and molecular data. (2) The putative traits of the last common ancestor (LCA) of Hominini and extant Panini. The models for the LCA can be constructed only on the basis of the fragmentary fossils of the earliest hominins (ErH) and on the basis of the morphology and behavior of

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B. Pawłowski (✉) • W. Nowaczewska
Department of Human Biology, University of Wrocław, Wrocław, Poland
e-mail: bogus@antropo.uni.wroc.pl; wnowacz@op.pl; nowacz@antropo.uni.wroc.pl

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extant apes. (3) The environment in which the ErH lived and could have been exposed to some specific selection pressures. (4) The hypotheses for the selection pressures for bipedality (SPfB), which is the main diagnostic trait of the hominin clade. Some arguments for and against suggested SPfB according to different hypotheses will be presented. (5) The putative selection pressures related to the dental features of ErH. A much more difficult task is inferring behavior (including the social structure) of ErH. Since the fossils of the earliest hominins are so scarce, inferences as to their behavior are possible mainly on the basis of some features of *Ardipithecus ramidus* (*Ar. ramidus*) representatives, i.e., their overall body size, sexual dimorphism in body size, and sexual dimorphism of the canines. Finally, the future perspective (e.g., through closer integration of paleoanthropology and genetics) for determining the first appearance of derived hominin traits and the selection pressures that acted upon them is discussed.

Introduction

The theory of evolution with its central tenet of Darwinian natural selection provides the scientific framework that gives the opportunity to understand the evolution of all life-forms including the hominins. Some lineage-specific phenotypic traits that can be observed in the fossil record or in living organisms ought to be explicable by certain selection forces. It is assumed that the traits that appeared and were perpetuated in some lineages were adaptive, i.e., were related to an improvement in relative reproductive success or in overall biological fitness, in relation to the specific physical or social environment. The factors that contributed to higher reproductive success of organisms that had some novel phenotypic feature are called selection pressures, and they can act either on morphology, physiology, or behavior. Natural selection is a process by which new adaptive traits (e.g., morphological, physiological, or behavioral) evolve and persist. In a population with heritable variation of traits, this can lead to phenotypic changes over consecutive generations. Although such processes as genetic drift or any other nonselective (random) forces may act on organisms and cause some lasting effects, it is mainly natural selection that produces long-term directional change (Ward 2002).

In the Late Pliocene, when hominins developed Paleolithic technology and became to some extent dependent on culture, they were released from some previously effective selection pressures (e.g., stone tools and the ability to control fire could have dramatically weakened the effect of predation pressure). However, before these inventions, i.e., in the Late Miocene and for most of the Pliocene, hominins were exposed to natural selection factors in the same way as other organisms. This means that for a large part of our evolution, human ancestors were constrained and directed by similar natural pressures to those acting on other organisms. The main types of selection pressures acting on the ErH might have been related to variability in climatic conditions and change in habitat, which can be driven by climate change and is usually strongly related to the types of food available, to predation or sociosexual factors (including sexual selection), and to biomechanical or energetic constraints.

In the early stages of hominin evolution, some specific features emerged that demand evolutionary explanation (e.g., bipedalism and certain dental features). There are, however, a few serious difficulties with the reconstruction of the selection pressures for hominin emergence. Reconstruction of the selection pressures that triggered the Panini–Hominini (P-H) split is today a somewhat more difficult task than it was only 15–20 years ago. This is because in the last two decades, we have gained new fossils that make the picture of human evolutionary tree more difficult to determine. What is more, some fossils attributed by their discoverers to the hominin clade are controversial in terms of the interpretation of features that may be homoplasies or retained hominoid primitive features (Wood and Harrison 2011). The most controversial of these is *Sahelanthropus tchadensis*, dated at over 6 Ma (Brunet et al. 2005), for which we have only craniodental material that was found ca 2,500 km west of the African Great Rift Valley (traditionally seen as the cradle of the hominins). This form exhibited small upper canines (worn at the tip) and the position of the foramen magnum suggests that this form was bipedal. These two traits were recognized as principal indicators of its hominin status (Brunet et al. 2005). Some authors, however, disagree that this form is a hominin and contest the inference, made on the basis of the position of the foramen magnum, that it was bipedal (Wolpoff et al. 2002). Less controversial the earliest hominin is *Orrorin tugenensis* from Lukeino Formation, dated to between 6.2 and 5.6 Ma (Senut et al. 2001; Pickford et al. 2002). Its remains include 13 specimens (fragments of hand, arm, and lower limb). The discoverers of *Orrorin* argued that the dental morphology of this form was "apelike" (its upper canine resembles that of a female chimpanzee) (Pickford et al. 2002). Based on morphology of its femur (BAR 1002'00), humerus, and manual phalanx, it is claimed that *Orrorin* possessed the adaptations both for bipedal locomotion and arboreal climbing (Senut et al. 2001; Pickford and Senut 2001; Richmond and Jungers 2008). Another genus widely attributed to the earliest hominins is *Ardipithecus*, containing two species: *Ardipithecus kadabba* (Haile-Selassie et al. 2004) from Central Awash Complex and the Western Margin, Middle Awash in Ethiopia, dated between 5.8 and 5.2 Ma, and the better-known *Ar. ramidus* dated to 4.4 Ma from the Afar Rift region (northeastern Ethiopia) (White et al. 2009). A relatively complete skeleton of the latter species (ARA-VP-6/500 – Ardi) provides data for the reconstruction of the earliest stages of human evolution and allows suggesting the putative traits of LCA of the Hominini and Panini clades (White et al. 2009). The preservation state of Ardi makes possible the comprehensive study of locomotion, morphology of the teeth, body size, and even sexual dimorphism of the earliest hominins.

The presence of the small canines and the lack of the C/P3 honing complex (characteristic of chimpanzees) in *Sahelanthropus* and *Ardipithecus* are traits they share with later hominins and are described as most indicative of their hominin status (Wood and Harrison 2011). However, as noted by Wood and Harrison (2011), the traits mentioned above are also visible in a number of Late Miocene

Eurasian hominids, and they probably developed in response to dietary behavior changes, induced by ecological conditions. We cannot then reject the possibility that a similar evolutionary response also took place in African Late Miocene hominids. There is similar problem with postcranial evidence for bipedalism in the earliest hominins and in European Late Miocene *Oreopithecus bambolii* (Wood and Harrison 2011). All these observations indicate that recognition of the earliest unquestionable hominins is still a difficult task. One cannot exclude the possibility that the currently ascribed traits to the earliest hominins will appear to be also the features of other members of hominid lineage (e.g., chimpanzee). Only new discoveries of more complete skeletons of Miocene African hominids would help to resolve this issue.

Another problem with the early stage of hominin evolution concerns methodology. Each new trait that appeared in ErH could be a real adaptation that emerged under some specific selection pressure, or it could be a trait that appeared as a side effect of some other functionally adaptive trait. If a new trait that was not under direct selection pressure later acquired some new function, it is called an exaptation. An exaptation – the term was coined by Gould and Vrba (1982) – is thus a trait that was not designed by selection. The appearance of such new by-products, nonadaptive traits, could be due to the effects of pleiotropy. When strong selection acts on a feature determined by a particular gene and if this gene is also responsible for some other feature, the latter feature can emerge irrespective of its adaptiveness and without any specific selection pressure on that particular trait. Thus, the presumption that all anatomical or behavioral traits are adaptively informative (Hlusko 2004) does not always need to be true. This also means that some morphological traits are not independent and should be analyzed as if they were dependent (Hlusko 2004) and not the effect of different selection pressures on each of the new features. We must then be aware that, the case of some derived hominin traits, one can be faced with side effects that were only later co-opted for a new function and which at the time of their evolutionary appearance were not selected specifically for the function they later acquired.

All this makes the reconstruction of the selection forces that triggered the P-H split a very difficult task. To try to decipher the selection pressures that led to hominin emergence on the basis of our present knowledge, the following problems will be addressed in this chapter:

1. The time when the P-H split could have taken place.
2. The putative traits of the last common ancestor of hominins and chimpanzee.
3. The environment in which the ErH lived and was exposed to specific selection pressures.
4. Possible hypotheses for selection pressures for bipedality, the main diagnostic trait of the hominin clade.
5. The putative selection pressures related to the dental features of ErH.
6. Whether on the bases of paleoevidence and socioecological rules, we can infer something about the behavior and social structure of the ErH (inferences from body size, sexual dimorphism in body size, and from canine size in ErH).

This chapter concerns the problem of selective forces that might have been related to hominin emergence and that could have shaped this evolutionary lineage at the stage of the early hominins, i.e., before 3.0 Ma. The selection pressures for the traits that appeared in the genus *Homo* at the end of Pliocene or in Pleistocene will be not analyzed here (e.g., brain size increase, rate of enamel formation, longer development and growth time span, language or cultural inventions, including stone technology, for which the oldest evidence we have comes from ca. 2.5 to 2.9 Ma).

When Did the Hominin Lineage Diverge from the African Extant Hominoids?

Early in the second half of the twentieth century, it was thought that the human lineage diverged from the lineage of living apes sometime between 10 and 15 Ma. This very early date for the origins of hominins was set in view of the strong peculiarities of humans, which were then seen as needing a long time to evolve, and because of the mistaken inclusion of the thick-enameled Miocene Asian ape *Ramapithecus* in the human evolutionary tree. Only in the late 1960s did pioneering molecular analyses (Wilson and Sarich 1969) reveal that the human–great ape split must have taken place at a much later date. The reassessment of *Ramapithecus* taxonomy and a stricter approach to all Miocene and Pliocene hominoid fossils from Africa confirmed that in fact there is no good fossil evidence of hominins before 7–5 Ma. Fossils found later and many new molecular results confirmed that dating. It now seems that there is a quite high concordance between the two kinds of evidence. Although in a range of molecular analyses the split was assessed from 3.6 (Easteal and Herbert 1997) to 13 Ma (Arnason et al. 1998), the bulk of analyses indicated either 7–5 Ma (Glazko and Nei 2003) or more extent 4–8 Ma (Wood and Harrison 2011). It is now generally held that for calculating the time of the human–great ape divergence, nuclear genes are a better guide than mtDNA. The evolutionary changes in mtDNA over time vary among different lineages, and for time estimation, we should use genes that follow a global molecular clock (Glazko and Nei 2003).

Based on the results encompassing the comparison of the genome sequence of the western lowland gorilla with the genomes of the extant hominoids (including *Homo sapiens*), Scally et al. (2012) considered the variation in past mutation rates (10^{-9} mutations per bp per year in the common ancestor of great apes and possibly $0.5\text{-}0.6*10^{-9}$ afterwards) and suggested that the human–chimpanzee split was between 5.5 and 7 Ma and human–chimpanzee–gorilla speciation between 8.5 and 12 Ma.

The majority of paleoanthropologists now agree that hominins appeared between 5.4 and 7.0 Ma. If the controversial Miocene taxa *Sahelanthropus* and *Orrorin* are unambiguous hominins, then this divergence would have taken place closer to 7 Ma than to 5 Ma.

Molecular data also bring an interesting perspective to selection intensity in the hominin and panin clades. The hominin lineage very likely underwent a reduction in effective population size after the divergence from the chimpanzee clade (Chen and Li 2001). This would indicate that our lineage was exposed to more intensive selection pressures than other hominoids. Furthermore, comparative genetic studies also indicate that the speciation event that gave rise to hominins and chimpanzees did not involve an extended period of gene flow between the emerging species (Wakeley 2008). Thus, it is very likely that this speciation was allopatric, i.e., related to geographic isolation of these two clades. This is in contradiction to Navarro and Barton (2003), who suggested that there was a relatively long period of gene flow in collinear chromosomes and therefore hybridization between ErH and its closest contemporary African ape (the ancestral chimpanzee). The long period of genetic exchange between these lineages was also suggested by Patterson et al. (2006), who estimated that human–chimpanzee speciation occurred before 6.3 Ma. These results were, however, later contested by Wakeley (2008).

We can tentatively conclude that knowing the estimated time of hominin emergence and the ecological circumstances of its occurrence in Africa allows reconstructing and perhaps identifying a small pool of possible selective factors that could have driven the P-H evolutionary split.

Last Common Ancestor

One way to infer the nature of the selective forces that were the main causes of the emergence of the hominin lineage from the species described as the "last common ancestor" (LCA) of humans and chimpanzees would be on the basis of the best available knowledge about the morphology of LCA, about the first derived traits that appeared in the earliest hominins, and about the place and environment in which the earliest hominins and the earliest representative of the chimpanzee lineage appeared. Unfortunately, at present, remains of African Late Miocene great apes among which LCA could be found are scarce (Suwa et al. 2007). This means that it is possible to construct models for the LCA on the basis of the fragmentary ErH fossils and on the basis of behavioral ecology of extant apes. It is also possible to infer the nature of the selective forces that existed at that time, because we have some information on the biotopes in which the ErH lived. However, one must be aware that there is no certainty that ErH really emerged in the areas and in the habitats from which we have fossil evidence of these forms.

Previously it was assumed that in cranial capacity, facial or dental features, as well as in postural ability, the LCA generally resembled the extant African apes. This form was described as living and foraging in the African tropical rainforest and using knuckle-walking locomotion on the ground (Richmond et al. 2001). The new specimens of the *Ar. ramidus* changed the views on the morphology and behavior of the LCA of human and chimpanzee lineages. The morphology of the skeleton of *Ar. ramidus* was not transitional between *Australopithecus* and its hypothetical apelike ancestor (earlier considered as similar to chimpanzee) (Lovejoy 2009; White et al. 2009). The traits exhibited by *Ardipithecus* indicate that the LCA probably had a low degree of sexual dimorphism, lacked specializations for knuckle-walking and suspension, had relatively thin enamel in the postcanine teeth, and had an omnivorous/frugivorous diet (Lovejoy 2009; White et al. 2009).

Although currently there are more remains of *Ardipithecus*, there is still an inadequate number of fossils and an absence of an archaeological record which would allow scientists to determine the social structure of the LCA. To reconstruct the behavior and reproductive strategies of the LCA, both parsimony and known socioecological rules are usually used for different behavioral traits present in the extant hominoids. Some scientists claim that the LCA and ErH were behaviorally most similar to the extant chimpanzees (McGrew 2010), but others contest this assumption (Sayers et al. 2012). Taking into account *Ardipithecus* body size and canine size dimorphism, the chimpanzee model might not be the best for inferring the LCA social structure. In order to infer social system of LCA and to avoid the chimpanzee referential doctrine, one should consider the characteristics, present in all extant African hominoids, such as:

- Male philopatry and female exogamy
- Male kin bonding social groups and coalitionary behavior
- Relatively complex interpersonal interactions
- Polygamy

These forms were also relatively intelligent and might have even used some rudimentary tools (view strongly supported by McGrew 2010). If the earliest hominins were sexually dimorphic in body size, the dinichism of LCA could be also inferred. Females could have had smaller home ranges and a somewhat different diet, e.g., as a smaller form, they could have more frequently used trees not only to escape from predators but also as a source of food and shelter.

Knowing the main evolutionary morphological adaptations that appeared in hominin evolution allows scientists to concentrate on the features that are distinctive of our close living relatives (the great apes). On the basis of this knowledge, modern Darwinian theory allows to make intriguing inferences about the selective pressures that could well have been responsible for the new (i.e., derived) traits that characterized the emergence of hominins.

Climate and Environment at the Time of Hominins' Emergence

There is a general premise that shifts in climate alter habitats and thus constitute selection pressures leading to speciation (DeMenocal 2004). It is known from many evolutionary lineages for different animals that key turnover events took place during times of climatic and ecological change (for more detail about climate influences on hominin evolution, see Vrba, chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). Until the late 1980s, it was assumed that the earliest hominins lived in open savanna environments and that the biotope they inhabited was a principal factor in the emergence of the hominins. The change of the east Africa environment to a more open, drier, and cooler habitat has been proposed as a main cause for the most important adaptive changes in hominins' evolution during the Plio-Pleistocene ("savanna hypothesis") (Vrba et al. 1989). However, with the addition of new paleoecological data from hominin fossil sites dating from the Late Miocene to the Early Pliocene, this hypothesis has been seriously undermined. We realize now that ErH lived in more mixed or wooded settings (Cerling et al. 1997; Brunet et al. 2005; Le Fur et al. 2009; WoldeGabriel et al. 2009; Blondel et al. 2010) and that the widespread expansion of more open environments in Eastern and Southern Africa took place a few million years after the emergence of bipedality (e.g., DeMenocal 2004, 2011).

Between 4 and 1 Ma, the main faunal turnover in the Turkana Basin occurred at four main periods: 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Ma (Bobé and Behrensmeyer 2004). The second and third intervals seem to coincide with the presence of *Paranthropus*, and the last one with grassland expansion and the first appearance of *Homo ergaster*. Pollen analysis also indicates that it was only after ca. 3 Ma that expansion of xeric vegetation took place (Dupont and Leroy 1995). Also, stable isotopic analyses of pedogenic carbonates from Turkana and Olduvai indicate a step-like increase in open habitats ca. 1.8 Ma (Cerling 1992). There is evidence that climatic and habitat changes triggered selection pressures that resulted in the emergence of *Paranthropus* and *Homo* and that they also triggered selection for the origin of other hominins (DeMenocal 2011).

Reed (1997) reconstructed Plio-Pleistocene habitats on the basis of the analysis of mammalian fossil assemblages. She compared eight vegetative habitat types in order of tree density forests: closed woodland, woodland bushland transition, medium density woodland and bushland, open woodlands, shrubland, grasslands, and desert. It is not surprising that the percentage of arboreal locomotion decreases as these habitats progress from forest to desert. Using fossil mammals from different African sites, Reed (1997) showed the relationship between habitat type and two ecovariables (locomotor and trophic). These two variables proved to be better indicators for habit differentiation than body size. According to her analysis, the percentage of arboreality and frugivory between 3.6 and 1.8 Ma in East Africa demonstrates closed to open woodland habitats. Only later does it drop to percentages indicative of shrub and grassland. All this means that there is more evidence that climatic and habitat changes triggered selection pressures that resulted in the emergence of *Paranthropus* and *Homo* than that they triggered selection for the origin of earlier hominins.

Paleobotanical and faunal evidence clearly indicate that the sites bearing fossils of *Orrorin* (Pickford et al. 2002), *Ardipithecus* (WoldeGabriel et al. 2009), *Au. anamensis* (White et al. 2006), and *Au. afarensis* represent mainly tree-dominated habitats (predominantly closed woodland). Although *Au. anamensis* (Leakey et al. 1995) and *Sahelanthropus* (Vignaud et al. 2002; Le Fur et al. 2009; Blondel et al. 2010) probably lived in more mosaic environments (gallery forests at the edge of lakes and savanna and grassland away from lakes), the places where they were found are related to a lacustrine type of gallery forest. These new data displace the long-held idea that bipedalism first emerged when climate change forced our ancestors to live in open environments. The "savanna hypothesis" gained a serious opponent called the "forest hypothesis" (Rayner et al. 1993), which states that it was dense vegetation that played an important role in the evolution of early hominins. It is the forest hypothesis that explains why ErH retained upper limb morphology with the functional capacity to climb trees (see next section). Data from western and southern Africa clearly indicate that the savanna hypothesis may instead be applicable to the emergence of the *Paranthropus* and *Homo* genera and not to the divergence of hominins from other hominoids (Bobé and Behrensmeyer 2004; DeMenocal 2011).

The change to more open habitat cannot, however, be completely excluded as a possible factor that triggered the acquisition of upright posture and the appearance of hominin lineage. It is possible that this bipedality emerged in the open environment in another region of Africa that is a still unknown cradle of hominin origin. Although the distribution of grassland before the Pliocene remains unclear, open habitats were present in Africa from the Middle Miocene (Retallack et al. 1990). Paleobotanical studies show that grass-dominated savanna became widespread both in west and east tropical Africa in the Late Miocene (ca. 8 Ma) (Jacobs 2004). This is documented by pollen and carbon isotopes. In the Late Miocene, Asian monsoons also influenced North and East Africa (Griffin 2002), and there was substantial environmental change from dense woodlands to grasslands or open woodlands in Asia (Barry 1995). Increased aridity around the Mediterranean and North Africa could also have led to the regional differentiation of apes. It is quite likely that such changes were not just coincidental with the rise of the hominins. Furthermore, if, as some claim (Rook et al. 1999; Wood and Harrison 2011), *Oreopithecus bambolii* in Europe was a biped and if this trait evolved in an open environment, then there is a strong argument that open habitat could be related to selection pressure that could have led to upright posture. All this means that there is no certainty whether the discovered fossil sites really represent the hominin cradle. They might just reflect later expansion of hominins from places with more open habitats.

New studies on the stable carbon isotopes in fossil soils from hominin sites in eastern Africa (Awash and Omo-Turkana basins) showed that since ca. 7 Ma woody cover was less than 40 % at most hominin sites examined (Cerling et al. 2011). This would mean that over the past six million years in eastern Africa, open habitats predominated. This result is surprising because the carbon isotopes analysis from the teeth of several *Ar. ramidus* individuals showed that they consumed C3 plants in woodlands or in patches of forests (Louchart et al. 2009; White et al. 2009). Furthermore, these hominins' bearing sites were rich in fragments of fossilized wood, and the analyses of the isotopic paleosol compositions indicate wooded conditions (WoldeGabriel et al. 2009). This might, however, be reconciled with time-frame results obtained by Cerling et al. (2011). They found that from Late Miocene to Early Pliocene (about 5.7–4.4. Ma) in Awash Valley and between 7.4 and 5.7 Ma in Omo-Turkana Basin, there was sparse wood cover. They also indicate that in this region of Africa, there was expansion of woody vegetation during the middle Pliocene. The same authors suggest that open habitats were associated with presence of the earliest hominins and that *Australopithecus* lived in more wooded environments. If they are right, it means that the emergence of the hominin clade could be associated with the significant shift in habitat conditions occupied by ancestors of the first hominins and that the "savanna hypothesis" may be reinstated as a potential hypothesis explaining the appearance of the bipedality. Further data are needed to resolve this problem.

Apart from two "habitat selection" hypotheses, there is also the "variability selection" hypothesis (Potts 1998), which is discussed in detail by Vrba. This hypothesis says that climate-driven habitat fluctuations over the last 6 Ma in Africa created disparity in adaptive conditions and caused habitat-specific adaptations to be replaced by morphological and behavioral adaptations to complex environmental changes (Potts 1998, 2012; Donges et al. 2011). It points to environmental instability as a main factor of selection among hominins for higher plasticity and new "multihabitat" adaptations. The crucial adaptations of the hominins seem to confirm that this group became adapted to variable environments. Bipedal locomotion and the retained tree climbing ability of the australopithecines made it easier to move relatively effectively both in densely forested and in open habitats. Dental traits adapted to hard and soft food, large brain volume, complex social behavior, and cultural adaptations in *Homo* permitted flexible responses to quite a wide diversity of climatic and habitat conditions.

Although the variability hypothesis is very attractive and seems to explain the high plasticity of early hominin morphology adapted to different habitats, behavior, and later technological inventions, it is not in line with the basic selection mechanisms working in relation to the acting present environmental and social conditions. Unless environmental changes happened really fast, it is hard to believe that for organisms with a generation time of 16–20 years (and for early hominins even less: 10–14), in a period of 40–100 thousand-year cyclicity, selection would keep costly adaptations for conditions prevailing in the distant future. One could also ask how the proposed frequent periodicity worked in the lineages of any other extant taxa.

Bipedal Locomotion as the Most Difficult Trait to Explain for the Early Hominins

There are many long-standing questions in paleoanthropology, but one of the most fundamental is why, in one lineage of hominids (but controversial *Oreopithecus*), selection promoted a new form of locomotion. Bipedalism is the hallmark trait for hominin evolution and its evolution poses a great conundrum for paleoanthropologists. The explanation of the emergence of this trait in human earliest ancestors is important, because this new locomotor pattern probably made possible (i.e., was a preadaptation to) the next great evolutionary jump, the emergence of the genus *Homo*, with its relatively bigger brain and with a postcranial anatomy almost indistinguishable from ours.

We neither want to address here the morphological and biomechanical aspects of bipedality nor to discuss the debate on the differences in bipedal locomotion between different forms of Hominini. What we want to touch on in this chapter are the putative selection pressures for the emergence of this unusual, for primates, way of locomotion and the putative pressures for enhancing the effectiveness of this locomotion in early *Homo*.

Many hypotheses have been put forward to explain bipedality. The first one came from Darwin, who suggested that it was the pressure for freeing the hands for the use of tools or weapons (Darwin 1871, p. 80). The problem with this, and with several later hypotheses, is that the proposed selective force could have been the consequence and not the cause of this evolutionary trait. Darwin himself was already aware of the risk of feedback loops between causes and consequences and recognized the difficulties of trying to disentangle them.

To think about the possible selection pressures for a new way of locomotion, it should first be considered what is already known about:

1. Locomotion of our pre-bipedal ancestors
2. Time and possible place where bipedality could have emerged
3. Climate and habitat in the areas where bipedality could have arisen

(Ad 1) Two main hypotheses have been proposed earlier on the prevailing locomotion of our pre-bipedal ancestors: brachiation (hylobatid-like) and terrestrial knuckle-walking (chimpanzee-like). The newly discovered fossils of *Ar. ramidus* throw a new light on the problem of origin of the bipedality in the hominin clade. According to the discoverers of *Ar. ramidus*, these hominins moved in the trees using palmigrade clambering and walked upright on the ground in woodland habitat, but their terrestrial bipedality was more primitive than that of *Australopithecus* (Lovejoy 2009). *Ar. ramidus* skeletons lacked any traits characteristic of knuckle-walking, suspension, or vertical climbing (e.g., the hand exhibited short bones of the palm and lack of the stiff wrist joints) (Lovejoy et al. 2009a). The pelvis of "Ardi" was useful for climbing and walking (e.g., upper blades were shorter and broader than in extant apes) (Lovejoy et al. 2009c). The foot of these hominins with opposable big toe exhibited the traits useful for upright walking both on the ground and on branches in the trees (Lovejoy et al. 2009b). *Ar. ramidus* remains indicate, then, that the LCA was probably not chimpanzee-like and that *Ar. ramidus* inherited arboreal capabilities from the LCA (White et al. 2009). The primitive traits of the *Ar. ramidus* skeleton provide a new perspective on the derived postcranial characters of *Australopithecus*. Relative to *Ar. ramidus*, *Au. afarensis* exhibited specializations visible in hand, foot, and pelvis, indicating that this hominin abandoned locomotion in the trees probably due to the emergence of new feeding patterns.

(Ad 2) There is direct evidence of bipedality from 4.4. Ma in *Ar. ramidus* and also from 4.2 Ma in *Au. anamensis*. As far as older hominins are concerned, there is still some disagreement. The foot bones fossils belonging to *Ardipithecus kadabba* (Haile-Selassie 2001) show mosaic morphology, and the position of the foramen magnum in *Sahelanthropus* is only indirect and weak evidence for bipedalism. Wolpoff et al. (2002) claim that the position of the foramen magnum excludes an upright position of the head and therefore made bipedality obligate in this form.

More certain diagnostic features for habitual bipedal locomotion are found in fragments of three femora of *Orrorin* (Pickford et al. 2002). If the earliest known hominin forms were really bipedal, this mode of locomotion, and therefore hominins themselves, must have appeared before 6 Ma. From a more conservative point of view, it might have appeared only between 5 and 4 Ma. Fortunately, accepting the first or the second date does not greatly influence our further analysis of the putative selection forces. This is because the habitats in which all ErH were found seem to be quite similar and therefore do not greatly change the inferences about the possible natural selection factors on the emergence of bipedality.

(Ad 3) The majority of the hypotheses on the SPfB are in a direct or indirect way related to the habitat in which the ErH lived. Thus, to verify all these hypotheses, we need to reconstruct the climate and habitats in which the ErH lived. On the basis of new data, some suggest that early stages of hominin evolution in Africa were related to open environments – a hypothesis that also predominated in the twentieth century. Since most evidence indicates that all forms older than 4 Ma lived in wooded habitats, currently the "woodland hypothesis" still dominates. Although those few fossil sites with Miocene and Early Pliocene forms for which there is paleoecological evidence provide quite a strong argument for a habitat in which bipedality could have emerged, this is nonetheless not unquestionable proof that bipedality and hominins evolved in such a habitat. The other problem is the question of how many times could bipedality have arisen among hominoids? The majority claim that this happened only once, but there are also proponents of more than one emergence of bipedality in hominoids (Rook et al. 1999; Wood and Harrison 2011). If *Oreopithecus bambolii* was also a biped (as Rook et al. 1999 claim) and if this form had nothing to do with the later hominins, this would mean an independent evolution of bipedality.

Having knowledge about these three points allows to narrow down the possible scenarios of selection pressures that could have been the cause of bipedality and most likely the evolution of the hominins.

Putative Selection Primers for Bipedal Locomotion

We know much more about the evolutionary stages of morphological adaptation to bipedal locomotion (see chapter "▶ Origin of Bipedal Locomotion," Vol. 3) than about the selection pressures involved in this process. The first difficulty is related to the uniqueness of this adaptation among primates. There is no living nonhuman species that could be used for comparison to allow distinguishing some potential selection factors promoting such a type of locomotion. The second problem lies in the fact that *Homo*-type bipedality emerged not in a short period of time or as an effect of one sudden event, but rather as a more gradual process (or rather with two evolutionary steps) over a long period of time. As far as postcranial anatomy is concerned, in all pre-*Homo ergaster* forms of Hominini, there is some combination of human and ape features (Wood and Lonergan 2008; Pickering et al. 2011).

This implies some degree of locomotor diversity and that at different stages of the elaboration of bipedal locomotion, different selection factors might have been involved. There are more plausible hypotheses regarding the pressures resulting in the changes related to the last stage of bipedalism that appeared in *H. ergaster* than regarding those related to the first stage. Furthermore, different selection pressures can be inferred, depending on whether all australopithecines were habitual bipeds or if they were only facultative bipeds.

The evolution of bipedalism requires adaptive explanation, not only because it is unique among primates but also because in comparison to quadrupeds this mode of locomotion has certain disadvantages (e.g., reduced speed and agility) and was related to the effective enforcement of some costly but necessary morphological changes. The question "why, then, did bipedalism evolve at all?" is crucial because it is very closely related to the answer to the question of what selection process caused the evolutionary appearance of hominins.

Many hypotheses have been advanced to explain the diagnostic and fundamental hominin trait of bipedality. So many concepts have been suggested that they can be divided into a few categories (Rose 1991; Niemitz 2010). Due to the limited space, and the limited plausibility of many of them, we are not going to describe all of them in detail. Some hypotheses violate the presently known temporal sequence of adaptations that appeared in our evolution; some seem to take consequences for causes; some suggest behavioral activity that can be performed as effectively when using, for instance, knuckle-walking locomotion; and still others are based on wrong presumptions about the habitat in which the earliest hominins lived. Furthermore, some hypotheses are very speculative, i.e., with no paleoanthropological evidence to support them, and some are very unlikely, e.g., due to the very weak or only very temporarily acting suggested selective pressure.

The majority of ideas are related to various behavioral pressures, e.g.:

a. Increasing viewing distance above tall grass (Oakley 1954; Dart and Dennis 1959)
b. Grass seed eating (Jolly 1970)
c. Freeing hands for using tools or weapons (Etkin 1954; Washburn 1967)
d. Load carrying (Preuschoft 2004) – but the same selector is also suggested only for the later *Homo* body proportions (Wang and Crompton 2004) – or more specifically carrying food (Hewes 1961; Isaac 1978; and in the sexual and reproductive strategy model of Lovejoy 1981) or tools and other valuable objects (e.g., unpredictably available food) Carvalho et al. 2012
e. Hunting or scavenging (Rodman and McHenry 1980)
f. Bipedal threat display (Livingstone 1962; Jablonski and Chaplin 1993) or "fighting from a bipedal posture" (Carrier 2011)
g. Terrestrial feeding postures when harvesting on small fruits of low, open-forest trees (Hunt 1994)
h. Walking and running (Jungers 1988; Bramble and Lieberman 2004)
i. Stone throwing (Fifer 1987; Dunsworth et al. 2003)

On the base of current knowledge, some of these hypotheses can be excluded (or treated as only of historical interest). This is because bipedality predated the use and manufacturing of stone tools (argument against c) and probably did not evolve in an open environment as was once assumed (a, b), and it predated robust hominin dental complex (b), predated hunting (e) and social structure changes, which could be related to provisioning females with meat food (d). Because of the high energetic cost of load carriage, infant carrying was also unlikely as precursor to bipedal locomotion (Watson et al. 2008). The hunting hypothesis (Brain 1981) can be applied as a selection force only for Late Pliocene hominins. ErH were rather the hunted than the hunters, and this also means that predation pressure on ErH in Late Miocene and in most of the Pliocene could have been quite strong and therefore could have influenced hominin evolution. The main predators of our ancestors were probably the leopard (*Panthera pardus*), saber-tooth felids, and possibly hyenids. Only very rarely in extant apes are such behaviors as throwing objects manifest (i) or bipedal display (f); thus, these factors are a very unlikely selection pressure to posture habitual bipedalism (against (i) and (f)). Although aggressive behavior can be associated with locomotor bipedalism, it is observed mainly in male chimpanzees in captivity (Thorpe et al. 2002). The other argument against this hypothesis (f) is small dimorphism in the body size of the *Ar. ramidus* and therefore probably low intermale aggression in the early hominins.

The cost of running for the type of bipedality used by ErH was probably higher than the cost of walking; therefore, possible selection for *Homo*, such as bipedal running, was rather an unlikely pressure for the emergence of bipedality. Biomechanical and energy saving hypotheses are usually proposed for the more humanlike bipedalism in *Homo* (Preuschoft 2004; Ruxton and Wilkinson 2011a).

The analysis of relative thumb length in *Au. afarensis* (Alba et al. 2003), however, reveals a similar proportion to that in present-day humans. This would mean a high precision grip capability in *Australopithecus* and would therefore be a strong argument for the hypothesis of the evolutionary causes of bipedality under the selection for manipulative skills in these hominins. Although this would support Darwin’s proposal (c) or others related to freeing the hands (b, d, e, i), one should remember that with these particular hypotheses, there is also the problem of the possible reciprocal causation of causes and consequences.

The second group of hypotheses is related to morphological, biomechanical, and/or physiological response to the physical environmental influences. One theory that in the 1980s seemed quite probable was the hypothesis of the avoidance of thermal stress (by decreasing body surface exposed to the direct overhead sunlight during midday, which allowed increased daytime foraging) in open environments where there is a strong diurnal insolation. This was first suggested in 1984 and later elaborated by Peter Wheeler. Since this hypothesis is inextricably related to open habitats, it is rather unlikely explanation for the origin of bipedality in ErH (Ruxton and Wilkinson 2011a). It would rather be applicable to the new adaptations that probably appeared only in the genus *Homo*, e.g., fur loss and elaborate thermoregulation by eccrine glands or endurance running (Ruxton and Wilkinson 2011b).

Another hypothesis is the very controversial idea of the aquatic or semiaquatic ape (Hardy 1960; Veerhaegen 1985; Morgan 1997), which states that upright posture appeared as an effect of selection for breathing air and for streamlined body shape in hominins who spent a lot of time in sea water, where they had to dive for food. This hypothesis also explains loss of body hair, brain size increase, and increase of subcutaneous fat tissue and newborn size (and even long hair on the head) as adaptations to the aquatic environment. It is a very speculative hypothesis, without fossil evidence, any similar reference within the primate order, and knowledge about the long time span sequence in the appearance of all these traits in Hominini. There is, however, also a more likely scenario that is related to littoral wading and is called "shore dweller hypothesis" (Niemitz 2010) and "waterside dweller" (Veerhaegen et al. 2007). These hypotheses are based on suggested advantages that could favor wading behavior and investment in high-quality food collection on shorelines. It also assumes that the ancestor of human clade was ecologically nonspecialized. This hypothesis is interesting and seems to be in accordance with the suggestions about omnivorous diet of LCA (Suwa et al. 2009). But whether wading behavior could stimulate our ancestor to stand up and bipedal walking, as suggested by Niemitz (2010), is still debatable. Although the data on seafood reliance by hominins (Braun et al. 2010; Steele 2010) seems to support this scenario, more evidence to connect the origin of bipedality with wading is needed.

What seems to be a likelier selection force for bipedality is the hypothesis proposed by Hunt (g). Although in nonhuman primates bipedal posture or locomotion accounts only for less than 5 % of total locomotion, the majority of what is observed is related to food acquisition (Rose 1991). Studies by Stanford (2002) also provide new data on relatively frequent arboreal bipedal posture (arm assisted) by chimpanzees when foraging for small fruits (mainly figs). Although an earlier concept by Washburn (1963) was also based on the chimpanzee model and feeding adaptation in bipedal locomotion, it emphasized terrestrial (and not arboreal) bipedal posture as a preadaptation of ErH that emerged in savanna habitats. The new data on the ErH habitats and on arboreal bipedality by chimpanzees support Hunt's hypothesis. Limb-length proportions in australopithecines indicate that their bipedality was rather related to the less energetically costly walking than running. This seems to support the view that the primary pressure could have been related to the postural feeding bipedalism and walking between clumped food sources (Rose 1984; Hunt 1994). On the basis of skeletal biology and ontogeny, it is rather unlikely that bipedality would have evolved only as a result of pressure for stationary bipedal posture. Bipedal walking must have been involved (Ward 2003), for instance, as in chimpanzee who use bipedal locomotion for transporting valuable food and objects (Carvalho et al. 2012).

The other cue for solving the problem of SPfB is the body size of the ErH. The postcranial remains of *Ar. ramidus* indicate that these hominins were relatively small (White et al. 2009); thus, it is possible that bipedalism emerged in relatively small forms that were forced to undertake longer terrestrial or arboreal walking (McHenry 1984). If there was selection pressure for bipedal posture among small-bodied hominins in the food acquisition context, then one can postulate that this pressure must have been the strongest for young (smaller) individuals who had even more difficulties in reaching the food source when it was above their heads. If they very often had to use upright posture while feeding, and if the food was relatively closely clumped (close to each other), frequent raising up of the whole trunk and the arms and stretching of the legs could have been more energetically costly than moving between these closely distributed fruits on two legs. If food acquisition pressure holds true, the costs for the behavior mentioned above must have been higher than for bipedality. Furthermore, when one arm was needed to hold and bend a branch and the second to collect food, the pressure for bipedal postural behavior and slow bipedal movement would have been even stronger. For small infants and young individuals that were already independent from mother's milk, reaching highly positioned food could have been possible only with maximal extension of the body and arms. Together with the need to climb trees, such postural feeding would also explain why arms were not shortened and fingers were still curved at this stage of hominin evolution.

According to fossil data and the molecular clock and considering how much complex rebuilding was needed to walk bipedally efficiently, we can say that natural selection acted really rapidly on the transformation of the hindlimb in the earliest stages of hominins' evolution. The evolution of the upper limb, rib cage, or even vertebral column was, however, much slower. What may be then important in determining putative selection pressures on the bipedality is to determine whether early Hominini, apart from their upright posture, were also effective tree climbers. If arboreality was unimportant in early bipedal forms, one can assume that it was biotope change that could have influenced this dramatic change. In the case of retention of arboreal agility and parallel adaptation to both types of locomotion, i.e., until the appearance of *Homo*, one needs to consider different selection pressures.

Australopithecines retained relatively plesiomorphic upper-limb morphology, but what is hotly debated is the adaptiveness of this ErH trait. Although it is still difficult to explain the retention of this primitive apelike character, there are only a few possible explanations for it: stabilizing selection for skilled arboreality, evolutionary inertia, pressure for a new kind of arboreality, change of diet at the time when bipedality appeared, or some specificity of ErH locomotion.

The arboreal environments in which the earliest hominins lived indicate that they could have spent quite a lot of time as tree dwellers, which would seem to explain the retention of prehensility and primitive upper-limb morphology (Lovejoy et al. 2009a). The *Ar. ramidus* postcranium indicates palmigrade clambering in the trees and more primitive terrestrial bipedality than in *Australopithecus* (White et al. 2009). According to Lovejoy (2009), upright walking probably did not provide energy advantage for *Ar. ramidus*; thus, these hominins lacked many of the adaptations which appeared in *Australopithecus*. White et al. also suggest that the further musculoskeletal adaptations (visible in *Australopithecus*) associated with more advanced terrestrial bipedality might have been the response to carry foods, simple tools, and/or offspring.

Using forelimbs for support when feeding could be a possible selection for the upright stature, as Hunt (1994) suggests. Similar to apes, an upwardly directed shoulder joint in *Au. afarensis* indicates that this form could have frequently directed its arms upwards (Green and Alemseged 2012; Larson 2012). All this might mean that the early hominin morphology, in effect, was a compromise for different locomotor patterns. Living in forested areas is a strong reason to have the possibility of also exploiting arboreal food resources and, therefore, of retaining the capability to climb trees.

According to the basic pattern of the genetic mechanism of limb development, there is strong covariance between the morphology of the upper and lower limb. It might then be that it was strong selection for shorter toes that caused the shortening of the fingers in ErH (Hlusko 2004), and shortened fingers should not be treated as an indication of the lack of selection for arboreality in these hominins. Shortened fingers would be then a side effect for bipedalism and an exaptation for tool using and manufacturing.

Our grasp of the selection mechanisms that were related to the emergence of bipedality and hominins will increase as more new fossils are recovered both from the Late Miocene and Early Pliocene and with the advances in the understanding of developmental and epigenetic processes (Ward 2002; Larson 2012).

Selection Factors Inferred from the Teeth and Masticatory System of Early Hominins

In addition to bipedality, the second important set of traits that seems to be connected with the appearance of the Hominini and that allows us to reconstruct the putative selection pressures that triggered the human–chimpanzee split is found in a number of features of the dentition. Teeth are not only more abundant as fossils than bones are (and especially those bones that directly indicate the mode of locomotion), but they are also easier for inferring the selection pressures which acted directly on them. Current knowledge of the adaptive meaning of relative tooth size and shape, enamel structure and thickness, microwear, and canine size is much better than of bipedality, which is not directly detectable in the earlier-known fossil record. These traits, together with the general robusticity of the masticatory system, are related not only to body size but primarily to diet (Andrews and Martin 1991). Food type and availability, and the locations in which food could have been found, probably constituted strong selection pressures on hominin evolution.

The diet of the ErH can be inferred from the teeth of *Ar. ramidus*, *Ar. kadabba*, *Sahelanthropus*, and *Orrorin*. The morphology of the crown of *Ar. ramidus* molars was not similar to those characteristic of *Pan*, *Gorilla*, and *Pongo*, and the other traits of these hominins' dentition (e.g., the incisors that were not as large as in *Pan* and *Pongo*) imply a diet different from extant apes (Suwa et al. 2009; White et al. 2009). *Ar. ramidus* lacked the enlarged rear teeth of *Australopithecus* that have been interpreted as adaptations to abrasive diet (heavy chewing) in open environments. The co-occurrence of the small canines with small molar crowns in *Ar. ramidus* can suggest that small canines appeared early in hominin evolution within the context of a nonspecialized diet (White et al. 2009).

All hominins living before 3.5 Ma had teeth with thicker enamel than chimpanzees. From the functional point of view, this means that EH were better adapted to eat abrasive food than extant apes. The molars' enamel of the *Ar. ramidus* appeared thinner from enamel exhibited by molars of earlier hominins and *Australopithecus*; thus, in comparison to them, *Ar. ramidus* diet was less abrasive. It is worth to note that the Miocene African apes, which gave rise to both living African apes and hominins, had relatively thinly enameled teeth (but thicker than in *Pan*) (Suwa et al. 2009). According to Sayers et al. (2012), the dentitions of the extent *Pan* and *Gorilla* are derived from that of their hypothetical LCA – e.g., *Dryopithecus* and all earliest hominins (including *Sahelanthropus*, *Orrorin*, and *Ardipithecus*). They stressed that molars of the *Ar. ramidus* showed some important similarities with those of *Dryopithecus* and *Pierolapithecus* (Miocene taxa of great apes) including bunodont crowns with low cuspal relief and also greater enamel thickness than in chimpanzees (Suwa et al. 2009); thus, *Ar. ramidus* is more similar to ours and *Pan*'s LCA than chimpanzee. The reconstruction of the evolutionary history of enamel thickness in the case of Miocene apes is a very difficult task, because of the uncertainties concerning their phylogeny. Alba et al. (2010) suggest that thin enamel could have independently evolved several times in hominid phylogeny and that thick enamel can be considered as the symplesiomorphy of the great apes and human clades. If they are right, it would mean that LCA had thick teeth enamel.

Macro- and microscopic wear patterns in *Ar. ramidus* molars indicate that these hominins had less abrasive diet and did less masticatory grinding than *Au. afarensis* (Suwa et al. 2009). Recently, the dental microwear texture analyses of hominin cheek teeth in specimens of *Au. anamensis*, *Au. afarensis*, and *Paranthropus* showed that none of the *Australopithecus* and *P. boisei* teeth have surfaces indicating that these hominins were hard-object feeders. Only *P. robustus* had teeth specialized for a diet based on harder items (Ungar et al. 2008, 2010, 2012). The results of these studies were surprising, because although *Au. anamensis* and *Au. afarensis* were from different habitats, their teeth show similar pattern of microwear complexity. The structure (including the thickness of the enamel) and the pattern of wear of the crowns of *Ar. ramidus* teeth indicate that this hominin's diet was not specialized and was less abrasive than that of later hominins (Suwa et al. 2009). It is probable that the LCA of human and chimpanzee lineages had the same nonspecialized diet as suggested for *Ar. ramidus*, i.e., omnivory and frugivory.

The results of the isotopic analysis of *Ar. ramidus* tooth enamel indicate that these hominins consumed mainly C3 plants (~85–90 %) in woodland habitats and small patches of forest. Savanna woodland-dwelling chimpanzees' intake was more than 90 % C3 plants, and *Australopithecus* (robust and nonrobust) consumed more than 30 % C4 plants (Suwa et al. 2009; White et al. 2009). Carbon isotope analyses, including those of hominin teeth from 4.4 to about 0.8 Ma, indicate dietary diversity and complexity. *Ar. ramidus* had C3 diet similar to chimpanzees and *Au. africanus*, *P. robustus*, and early *Homo* consumed more than 50 % C3 plants and also nearly similar quantity of C4 foods (Ungar and Sponheimer 2011). Thus, earlier ideas about the increasing dominance of hard objects in the diet of early hominins have been challenged (Ungar and Sponheimer 2011). The shift from C3-dominated diet to more middling diet (nearly the same proportions of the C3 and C4 food in diet) observed from *Ar. ramidus* to later hominins suggests the expansion of the *Australopithecus* into more open habitats. Taking into account the recent discovery at Dikika (Ethiopia) of the stone-tool-inflicted marks on animal bones older than 3.39 Ma, one cannot exclude the possibility that some species of *Australopithecus* (e.g., *Au. afarensis*) used stone tools for meat and marrow consumption (McPherron et al. 2010) and that these forms had a more expanded geographical range than the EH.

The paleofauna, plant fossils, isotopic composition of soil samples and teeth all indicate that *Ar. ramidus* lived in woodland with patches of forest (WoldeGabriel et al. 2009). It is supposed that *Ar. ramidus* relied on a wider range of woodland foods than chimpanzees but did not like *Australopithecus* rely on open-biotope foods (White et al. 2009). All this seems clear when one look at the available fossils of *Australopithecus*, but inferring the putative dietary selection pressure acting on the P-H split is somewhat more complicated. *Ardipithecus* had still relatively thin enamel (White et al. 2009) and was forest dwelling, and these lines of evidence are against the prime-mover strong selection for a dietary change that might have triggered a P-H split. If, however, either *Sahelanthropus* or *Orrorin* was the first hominin, and both had relatively small canines and thicker enamel than *Ardipithecus*, then the possibility that the selection for a dietary shift was one of the causes for hominin emergence cannot be excluded. In that case, dental features would show the influence of dietary selection pressures from the very point of origin of the hominins.

According to the present knowledge of the dental features of ErH and the suggested hypotheses of selection pressure for upright posture, the most likely scenario for the selection pressure that triggered the P-H split would be adaptation to more variable food, including some clumped and small fruits that were easier for ErH to reach via an upright body position in the trees (Hunt 1994) or possibly from the ground. This scenario can also be inferred on the basis of the relatively small incisors in ErH (Suwa et al. 2009). This is because primates eating smaller fruits ingest them without extensive incisor preparation (Ungar 1994). Relatively longer thumbs in australopithecines (Alba et al. 2003) would support this hypothesis. However, unless more certain fossils of the ErH are found, to fully answer the question of whether selection for new diet was intimately connected with the P-H separation will not be possible.

Inferences About Behavior and Social Structure of the Early Hominins

Fossil evidence provides scientists with information about the skeletal or dental morphological features that appeared in the early hominins. A much more difficult task is inferring behavior (including species-specific social or mating structures) from these very scarce fossils. This is much easier for later forms of hominins (e.g., *Homo*) for which there are more fossils and such archaeological records as stone tools or animal bones with cutmarks. In general, paleoanthropologists have almost the same idea about the behavior of the earliest hominins as about the behavior of the LCA. Nonetheless, they try to use all possible hints to reconstruct the behavior and social structure of the ErH. With no direct evidence of early hominin social structure and behavior, one can only propose some models that are not in disagreement with the fossils. Apart from features of locomotion and diet that probably modified ErH behavior in relation to the ancestor, other aspects of behavior and social structure do not seem to be very different. What can be inferred about behavior or the mating system of the ErH is based mainly on overall body size, sexual dimorphism in body size, and sexual dimorphism of the canines.

Since fossils of the earliest hominins are so scarce, one can only infer their behavior on the basis of some features of new remains of *Ar. ramidus* and later *Au. afarensis*. Recently it was shown that *Ar. ramidus* exhibited less dimorphic skeletal body size than *Australopithecus* (White et al. 2009). This, similar to *Pan*, sexual dimorphism in size (SDS) in *Ar. ramidus* suggests a male-bonded social system. According to Sayers et al. (2012), the morphological traits of the "Ardi" skeleton indicate that the LCA was anatomically and behaviorally different from chimpanzees. In contrast, McGrew (2010) asserts that based on the current knowledge on chimpanzee behavior, one should infer the trait of our LCA. Below are putative selection pressures and behavioral consequences of body size and sexual dimorphism of the ErH.

Were There Any Selection Pressures on Body Size of Early Hominins?

Body size is very informative about animal socioecology, life history (see Zimmermann and Radespiel chapter "▶ Primate Life Histories," Vol. 2), and possible selection pressures that can act on differently sized animals. For example, smaller forms have more predators, smaller ranges, and less protection against hypothermia. The advantages of having a bigger body size are manifold: a lower predation risk, better control over the environment, higher mobility, bigger brain, longer infancy, and therefore longer time for learning and a longer lifespan. Disadvantageous consequences, however, are also present: longer gestation and infancy means longer maternal dependence, and more food and a bigger foraging area (home range size) are needed (Clutton-Brock and Harvey 1980). Without knowing the size of the LCA, it is difficult to speculate about any selection pressure for body-size change in the ErH. If they lived in a forested environment as their ancestors did, then it is rather unlikely that there was any pressure for changing body size that was independent from the pressure for greater bipedal biomechanical efficiency. What is known for sure is that a change in size did take place in the Late Pliocene, when *Homo* emerged.

Until the relatively recent discovery of "Ardi," early hominin body size and sexual size dimorphism were inferred from *Au. afarensis*, and the main reference fossil specimen was "Lucy" (AL-288), which had preserved ca. 40 % of the skeleton. Now these inferences can be made on the basis of most complete skeleton of the earlier and relatively small "Ardi." Only minimal dimorphism in size probably characterized "Ardi" and indicates that the common ancestor of human and chimpanzee presumably also exhibited the same trait. If this assumption is proper, the specific selection pressures that could have acted on body size and sexual dimorphism at this stage of hominin evolution cannot be suggested.

Sexual Dimorphism and Social Structure

Sexually dimorphic traits specific to hominins should also have been selected for in response to certain selection pressures. Analysis of SDS, and its changes in the hominin lineage, might then give some insight into the mating system and social structure of these forms. It is known from living primates that SDS reflects male–male competition for monopolizing the reproductive potential of females. Higher SDS is usually related to more intense male intrasexual aggression. Male body size is an investment in fighting abilities, and this investment is inversely related to the mating opportunities (Trivers 1972). Species living in a one-male group (e.g., gorilla) have the largest SDS, monogamous species (like gibbons) are monomorphic, and species living in multi-male groups (like chimpanzee) have moderate SDS. The difficulty with reconstructing the mating system in the earliest hominins is related to the lack of sufficient fossil data for the size of both sexes. Fragmentary fossils mean that sex assignment is made frequently only on the basis of size (and not on pelvic or cranial morphology). This may lead to overestimation of SDS.

The problem with inferring social structure, however, becomes complicated when one also takes into consideration dimorphism in canine size (CD). This feature can also be useful for reconstructing mating systems, as CD is often positively related to SDS and therefore might also indicate a higher level of intra-male competition. If SDS and CD were both large in ErH, behavioral inferences would be relatively consistent, indicating a polygynous reproductive system in these forms. The problem appears when, contrary to SDS which suggests a high intensity of competition, CD in hypothetical ErH is small and therefore contradicts a high male–male competition for females. To solve this problem, Plavcan and van Schaik (1992) distinguished four types of male–male competition that are connected with different SDS. In order of increasing SDS: (1) low frequency and low intensity (as in monogamous gibbons), (2) high frequency and low intensity (as in chimpanzees), (3) low frequency and high intensity (as in *Saimiri*), and (4) high frequency and high intensity (as in *Macaca mulatta*, *Papio hamadryas*). These authors claim that the SDS of ErH hominins fits well with type 2 here.

The best present model for SDS and CD and therefore social structure in the earliest hominins is *Ar. ramidus*. The lack of a projecting, daggerlike upper canine crown and absence of an apelike honing C/P3 complex (characteristic for chimpanzees), together with reduced canine size in *Ardipithecus* males, indicates a lower intensity of male–male aggression in this species than in extant chimpanzees. Although the canines of the earliest known hominins at about 6 Ma were slightly more primitive, they were similar in size to those of *Ar. ramidus* (Suwa et al. 2009). This indicates that male canine size was reduced by 6–4.4. Ma from an ancestral apelike condition which probably exhibited a honing C/P3 complex and a moderate chimpanzee-like difference in size between male and female canines (Suwa et al. 2009). Among other features, the big size of the upper canines is important in territorial defense and in male agonistic behavior. The "feminized" shape of the male canines in *Ar. ramidus* and in other early hominins has been interpreted as the result of sexual selection and an occurrence of the reproductive and social behavioral changes in hominin evolution long before brain enlargement and stone tool use (Suwa et al. 2009).

The dental traits and small SDS of *Ar. ramidus* justify ascribing to LCA minimal skull and body size dimorphism and moderate canine dimorphism, indicating male philopatry, weak competition between males, and probable male–female codominance (as in the case of *P. paniscus* and ateline species) (Suwa et al. 2009). The intense intermale aggression characteristics of *Pan troglodytes* or social structure of gorillas are then rather unlikely social models for the LCA (Lovejoy 2009; Suwa et al. 2009; White et al. 2009).

High variation in body size in *Australopithecus* within a single site indicates high SDS and strongly undermines the hypothesis of a monogamous mating system in these forms (e.g., as suggested by Lovejoy 1981) and its possible influences on the evolution of bipedality. Gordon et al. (2008) also demonstrated that *Au. afarensis* showed substantial level of sexual dimorphism (most consistent with that present in gorillas and orangutans), which is in contrast with human or chimpanzee-like level of SDS in this species, as earlier suggested by some authors (e.g., Reno et al. 2005). SDS in *Australopithecus* was also larger than in *Ar. ramidus* (White et al. 2009).

If the driving force behind SDS in anthropoids is sexual selection (Lindenfors and Tullberg 1998), it can be inferred on this basis that the social structure in the earliest *australopithecines* was not monogamous. Although smaller canines in male in these forms might indicate a lower selection pressure for fighting ability, they lived probably in multimale/multifemale groups. A new skeleton of a large-bodied *Au. afarensis* male (dated to 3.38 Ma) discovered in Ethiopia indicates sophisticated terrestrial bipedality (Haile-Selassie et al. 2010). It is then possible that the reduction of body size in *Australopithecus* females was the result of enhancing their cooperation, but male size could have increased in response to predation pressure, which became higher in more open habitats invaded by these hominins (White et al. 2009).

All presented evidence and inferences about social structure face also the problem of great variation in SDS or CD within one competition type. There are a number of polygynous species with a very slight degree of dimorphism both in body and canine tooth size (Plavcan 2000). Thus, inferring social behavior from sexual dimorphism in primates has proved to be ambiguous, and this means that all speculations on the ErH social structure based on SDS or CD should be treated with caution. It cannot be also excluded that the mixture of high SDS and low CD was a consequence of male predator defense and not strong male–male competition.

The primate species with higher frequency of conciliatory behavior (e.g., Tonkean macaques or bonobos in comparison to chimpanzees) have lower CD (Plavcan and van Schaik 1992). There is also a possibility that the lack of concurrence of marked SDS and CD implies a unique social system that is unknown among living primates.

One possible explanation of the canine reduction observed in ErH (*Ar. ramidus* and *Australopithecus*) is the relaxation of the selection pressure favoring canine use as a weapon in an intrasexual and/or antipredatory context. Furthermore, the selective forces responsible for canine reduction probably had nothing to do with their dietary function. The later possibility of using them as functionally equivalent to incisors could have been a by-product of canine reduction selected for other reasons (Plavcan and Kelley 1996). In the opinion of Leutenegger and Shell (1987), however, the lack of CD in australopithecines could have produced the effect of "dental crowding," which resulted from the selection for the increase of premolar and molar chewing surface area, and SDS was a result of relatively high intrasexual male competition. Unfortunately, past behaviors do not fossilize, and therefore, one cannot be certain about the mating system within the early Hominini.

Small-bodied hominins disappear from the fossil record ca. 1.7 Ma (McHenry 1994). This suggests that there was strong selection pressure for both female and male body size to increase. However, this increase was much larger for females (McHenry 1994). Thus, it is unlikely that it was sexual selection, for example, for monogamy, that caused the decrease in SDS. If the decrease of SDS had been related to selection for monogamy, one would have expected a reduction in male–male competition and thus male body-size decrease (Lindenfors and Tullberg 1998) rather than a large increase in female body size. It is more likely, therefore, that selection pressures could have been related to locomotion efficiency (longer legs enabled walking for longer distances, which was adaptive for both sexes) or to an antipredatory strategy, thermoregulatory demands (Ruff 1991; Wheeler 1992), or to giving birth to bigger and fatter newborns (Pawlowski 1998) with larger brains.

Future Perspectives for Determining the First Appearance of Derived Hominin Traits and the Selection Pressures Acting on Them

There is no doubt that the closer integration of paleoanthropology and genetics will in the future markedly advance our knowledge of the mechanism of hominin evolution. It is worth to note that the phenotypic traits described as unique to human lineage are commonly considered as the results of the selective pressures acting on human genome and the unique demographic history since the time of the divergence of the human and chimpanzee lineages (O'Bleness et al. 2012). Currently the rapid comparison of the numerous genomes within and between species is possible, and there are data on the draft genomes of several primate species including chimpanzees (*Pan troglodytes*), bonobo (*Pan paniscus*) (Prüfer et al. 2012), gorillas (Scally et al. 2012), and orangutans (Locke et al. 2011). It was, for instance, determined that 25 % of human genes contain parts that appeared closely related only to one of the two *Pan* species (bonobo or chimpanzee). The examination of these regions can help to determine the genetic background of the phenotypic similarities between humans and *Pan* and to assess the time of their evolutionary appearance. There is also the genetic evidence that LCA of human and *Pan* lineages possessed a mosaic of the traits specific to human, chimpanzee, and bonobo (Prüfer et al. 2012).

We are now in the "golden age" of exploration of the genetic changes and between-species differences that might contribute to the search for the emergence of the specific traits for human lineage. On the basis of the sequence changes that occurred at the rate greater than the rate of the neutral mutations, we are able to identify hypothetical evolutionary pressures. There are, however, still many challenges we face with (O'Bleness et al. 2012). Most problematic is difficulty in linking human-specific genomic change to human phenotype features. This is because to understand the genomic changes, one has mainly to rely on the observation of the variation and diseases that occur in modern humans (O'Bleness et al. 2012), although recently applied heterologous expression of human regulatory regions in mice allows detecting functions of genetic changes specific to human lineage (Prabhakar et al. 2008; McLean et al. 2011). An interesting example of using this method is the study of human accelerated noncoding region 1 (HACNS1) enhancer. This noncoding region is expressed in the anterior developing limbs of the mouse embryo, which could mean that HACNS1 might have contributed to the emergence of human bipedalism (Prabhakar et al. 2008; O'Bleness et al. 2012).

It can be supposed that identification of the genes or genomic regions more directly responsible for the traits that emerged in our lineage than those suggested now will be in the future easier and much more helpful for reconstructing the fine details of our evolutionary past. Finding the time of the appearance of different gene changes will allow to put a date to the emergence of given traits and to identify the particular selection pressures that were responsible for the appearance of different traits in hominin evolution. A good example of this issue is the assessment of the appearance time of the FOXP2 gene in human evolution. FOXP2 has been described as helping in learning the complex muscle movements important to speech and language in human (Enard et al. 2009), and it was suggested that the human version of this gene appeared about 500,000 years ago (Krause et al. 2007).

What is abundantly clear at the beginning of the twenty-first century is that in combination with these genetic approaches, our grasp of the mechanisms of hominin evolution will radically improve through the discovery and interpretation of hominin fossils uncovered in strata of Late Miocene and Early Pliocene ages.

Conclusion

The main focus of this chapter was the consideration of the main adaptive traits that appeared in the early hominins, paying particular attention to the putative selection pressures that could have triggered the hominin–chimpanzee split and then acted on the early hominins prior to the appearance of genus *Homo*. This task, however,

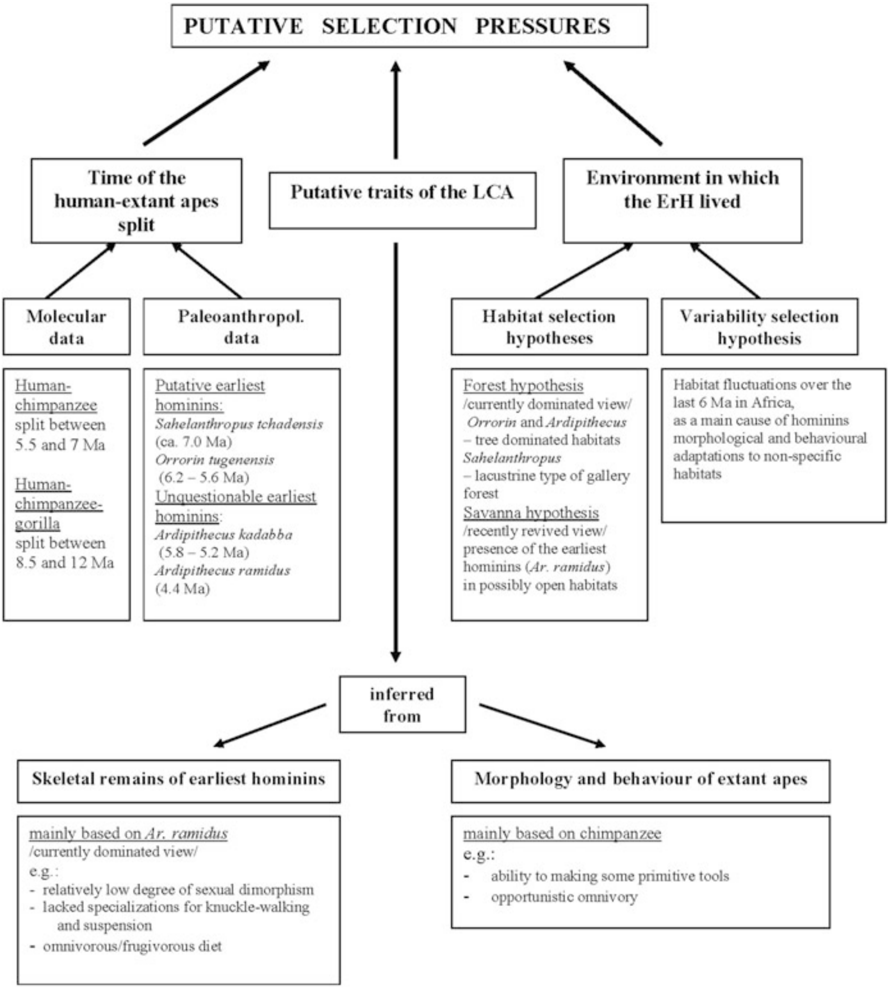

Fig. 1 The main types of data helpful in inferring the putative selection pressures acting on the early hominins. *LCA* last common ancestor, *ErH* the earliest hominins

is not easy. Although there is some general idea about the chronological sequence of the appearance in hominins of new (derived) morphological traits, the typically very fragmentary nature of the pre-hominin and early hominins' fossil record limits our ability to fully account for both the selection pressures acting on derived morphological traits and even more so for behavior of the earliest hominins (Fig. 1). It is obvious that the availability of only hard-tissue fossils restricts our possible understanding of the whole biology of these extinct forms. But paleoanthropologists can also have problems with determining the evolutionary mechanisms that were responsible for the appearance of main morphological hominins' features.

There is not even a clear pattern of the main changes in the earliest stages of hominins' evolution. The most certain trait, diagnostic for this clade, is bipedal locomotion, and this is certainly the trait for which a clear evolutionary explanation is really needed. Since it is the defining hominin trait, it is almost certain that explaining selection pressures for bipedality is concomitant with explaining the causes of the hominin–chimpanzee divergence. But unless the chronological order of the ErH is determined, the reconstruction of the main selection forces that led to the hominin–chimpanzee split will remain unclear.

The reconstruction of selection pressures responsible for hominin emergence would be easier if paleoanthropologists were dealing with a complex of traits that appeared at the same time than if the derived traits appeared at different times and were independent of each other. In the latter case we would need to analyze each trait separately, and there are possibly more selective pressures to be taken into consideration. When a few traits appear at the same time, it is usually much easier to propose a selective factor (the pool of such factors would be restricted) for a complex set of dependent traits. For instance, if the ErH became bipedal and at the same time acquired new masticatory adaptations to feed on abrasive food, then the habitat change hypothesis for bipedalism would be more likely as a putative selection pressure for hominin appearance. If *Orrorin* and *Sahelanthropus* were the earliest hominins, it could be inferred that bipedality could have arisen concomitantly with a dietary shift towards more variable diet, including more abrasive foods. Since they lived in a mosaic environment, and *Sahelanthropus* lived far from East Africa, one cannot exclude the possibility that the cradle of the hominins was much farther to the north that was originally thought and that it was in a more open environment in which bipedality and thus the hominins first emerged.

The knowledge of the sequence in which the different traits emerged is, however, not enough to exclude one selection factor for different traits. This is because the appearance of new traits can be related to a different speed of evolutionary response for the same selection pressure or can be related to different strength of the same pressure at different times. It seems unlikely that such a fundamental hominin trait as bipedality emerged a number of times independently. Other traits, such as size and body proportions, or bone and enamel thickness, seem to respond much faster to environmental selection pressure, so in our family tree, these traits might have changed in a different way in a few evolutionary lines. This notion is important because it is usually presumed that the evolutionary processes are parsimonious, which means that traits are difficult to change and evolve, and therefore, it is unlikely that one trait evolved independently in different lineages. However, such an easily evolvable trait as enamel thickening appeared under similar selection pressures, probably independently in the evolutionary lineages of at least a few Miocene hominoids.

When speculating about putative selection pressures, one should also remember to distinguish causes from consequences. It is easily possible to construct scenarios which confuse them. The problem is that in many cases, they are then difficult to disentangle.

The earliest stage of hominin evolution seems to be the biggest mystery and challenge of our entire evolutionary clade, and therefore, it should be no surprise that the theories of the selection pressures presented here are in part inherently speculative and highly vulnerable to adjustment in the light of new evidence. There is no doubt we need more ErH remains to find out whether some ErH skeleton traits were homoplasies or symplesiomorphies. This would allow to acquire much better knowledge about the traits of LCA (Wood and Harrison 2011). We can only hope that some fresh evidence will be gained soon and that it will allow to exclude some of the more unlikely selection pressure scenarios, thereby both narrowing the debate and at the same time making it more substantial.

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Origin of Bipedal Locomotion

William E. H. Harcourt-Smith

Contents

Abstract

Bipedalism is a highly specialized and unusual form of primate locomotion that is found today only in modern humans. The majority of extinct taxa within the Hominini were bipedal, but the degree to which they were bipedal remains the subject of considerable debate. The significant discoveries of fossil hominin that remains in the last 40 years have resulted in this debate becoming

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W.E.H. Harcourt-Smith (✉)
Department of Anthropology, Lehman College CUNY, Bronx, NY, USA

Department of Anthropology, The Graduate Center CUNY, New York, NY, USA

Department of Vertebrate Paleontology, American Museum of Natural History, New York, NY, USA
e-mail: willhs@amnh.org

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increasingly focused on how bipedal certain fossil taxa were, rather than on the overall process. Although the early hominin fossil record remains poor, evidence points to at least two distinct adaptive shifts. First, there was a shift to habitual bipedalism, as typified by certain members of *Australopithecus*, but possibly including earlier genera such as *Ardipithecus* and *Orrorin*. Such taxa were bipedal, but also retained a number of significant adaptations to arboreal climbing. The second shift was to fully obligate bipedalism and coincides with the emergence of the genus *Homo*. By the Early Pleistocene, certain members of *Homo* had acquired a postcranial skeleton indicating fully humanlike striding bipedalism. The final part of this chapter reviews why bipedalism was selected for. There have been many theoretical explanations, and the most robust remain those linked to the emergence of more varied habitats. Such an environmental shift would have involved strong selection for new behavioral strategies most likely linked to the efficient procurement of food.

Introduction

Bipedal locomotion sets modern humans apart from all other living primates. We are the only obligate bipeds among well over 200 extant primate species. It therefore stands to reason that this unusual and highly derived form of locomotion has attracted much attention from those who study human evolution. Current evidence points to anatomical traits strongly associated with bipedalism relatively deep in the hominin lineage (Ward et al. 2001) and well before the advent of other “traditional” human traits such as larger brains and tool use. This chapter reviews the current state of thinking on this unique form of primate locomotion.

In order to understand the origins of hominin bipedalism, one first has to understand the mechanisms that make it such an efficient form of locomotion in modern humans. In the first section of this chapter, I will briefly explore the nature of the modern human walking cycle and the associated anatomical traits that facilitate it. I will then explore the fossil evidence for the origins of bipedalism and speculate on the likely locomotor behaviors that preceded it. Finally I will discuss some of the theories surrounding why bipedal locomotion was selected for.

Locomotor Differences Between Modern Humans and Great Apes

Modern humans are fully obligate bipeds. After the first few years of life, bipedality is the sole form of locomotion in all healthy individuals. By comparison, the great apes do not have any one form of specialized locomotion. *Pongo* is almost exclusively arboreal, but its locomotor behavior is taken up by clambering, vertical climbing, brachiation, terrestrial fist-walking, arboreal quadrupedalism, and even some above-branch assisted bipedalism, although orangutans are best known to have a predilection for suspensory postures (Tuttle 1968; Thorpe and

Crompton 2005; Thorpe et al. 2007). Clambering, which accounts for over 50 % of observed locomotor behavior, mainly consists of forelimb suspension and hindlimb support and suspension (Tuttle 1968; Cant 1987). In nearly all respects *Pongo* can be considered to be an arboreal specialist.

The most important aspect of the African apes is that, unlike *Pongo* and modern humans, their specialization lies not in their tendency to be *either* arboreal or terrestrial specialists but rather on having a mosaic of different locomotor modes that suit different environments and situations. Field observations have shown that all three African ape taxa spend considerable time in both the trees and on the ground. The principal form of terrestrial locomotion is fast and slow knuckle-walking, where the legs do most of the propulsive work but a significant degree of body weight is borne by the upper limbs through the knuckles (Tuttle 1970). African apes spend a small degree of time walking bipedally, but only for relatively short periods of time (Tuttle 1970; Hunt 1994). *Pan* also spends a proportion of its time standing bipedally, mainly to collect fruit in tall bushes, but it is important to note that, even when doing so, individuals are partially supporting themselves with their upper limbs, which are grasping onto branches (Hunt 1994; Doran and Hunt 1995). When in the trees, *Pan troglodytes* has a particular predilection for using knuckle-walking to move along large branches (Tuttle 1970).

The Walking Cycle

The modern human walking cycle is characterized by two distinct phases: the *stance phase*, when the leg is on the ground, and the *swing phase*, when it is off the ground. The stance phase begins with the foot striking the ground, known as *heel-strike*. The knee is fully extended and the foot dorsiflexed, which results in the heel-striking the ground well before the rest of the foot. The foot then plantar flexes, and typically force is transmitted through to the substrate along its lateral border. The point when the body is directly over the weight-bearing foot is known as the *midstance phase*. The body then carries its forward momentum over the leg, at which point force moves medially over to the ball of the foot. At this point, strong muscular contraction of the plantar-flexors results in the ball of the foot pushing against the ground and eventually lifting away from it as the body continues to move forward. This action finishes with a final push-off of the big toe, known as *toe-off*. The leg is now off the ground and in the swing phase, with the knee and hip both bent so as to keep the leg off the ground as it swings forward to make the next heel-strike.

When chimpanzees walk bipedally, there are considerable differences (Aiello and Dean 1990). The knees and hips remain bent throughout the stance phase, and the foot is less dorsiflexed at heel-strike. This results in a gait that is an awkward “shuffling” movement, with marked mediolateral swaying of the body from step to step, that is often referred to as a “bent-knee, bent-hip” (BKBH) gait. Heel-strike itself is at best weak and is often almost immediately followed by much of the rest of the foot making contact with the ground. There is little in the way of the lateral to medial shift in force transmission to the substrate during the late stance phase, and often three or more toes leave the ground at the same time (Elftman and Manter 1935).

Associated Anatomical Differences Between Humans and Great Apes

A large number of anatomical traits are functionally related to bipedal locomotion, and it is the combination of these traits that allows this to be the sole form of locomotion in modern humans. Naturally it is sometimes hard to determine which traits specifically *facilitate* bipedal locomotion and which are more a *result* of it, but in terms of determining the locomotor affinities of fossil remains, it is fair to assume that, either way, many of these traits certainly *indicate* bipedal locomotion to a lesser or greater degree. Table 1 summarizes the major anatomical features associated with human bipedal locomotion, but a number of them warrant further discussion. In some cases, where particular traits relate to particular fossil specimens, there is further discussion in section "Fossil Evidence."

Some of the most radical morphological adaptations in the human skeleton that relate to bipedalism are found within the pelvis and lower limb. Compared to apes, the entire lower limb complex in humans has become highly remodeled to cope with the intricate dynamics of balancing an upright trunk while efficiently moving the body forward (Schultz 1930). Balance is a particularly important factor as at any point during the walking cycle, only one limb is actually in contact with the ground and has to bear the entire weight of the body and balance it accordingly. The minimizing of mediolateral swaying of the body during walking is therefore critical, as it acts to stabilize the body over the supporting leg and to reduce energy expenditure. Consequently, many of the traits associated with bipedal locomotion relate to two major factors: balancing the body as a whole and keeping the downward transmission of force as close to the midline of the body as possible.

In the skull there are two main osteological features related to bipedalism in modern humans. The semicircular canals have a larger vertical canal, which is thought to relate to more complex bipedal behaviors such as running (Spoor et al. 1994). The foramen magnum is also more anteriorly situated and horizontally orientated. This is a reflection of the more vertical positioning of the spine. Anterior positioning of the foramen magnum has recently been shown to relate to bipedalism in several lineages of mammals that have independently become bipedal (Russo and Kirk 2013). Below the neck, the spine of modern humans has a distinct "S" shape, caused by marked lordosis in the lumbar region, which helps to bring the center of the trunk's mass anteriorly (Aiello and Dean 1990; Fleagle 1999). The lower limb is considerably longer in modern humans than in great apes. *H. sapiens* has a low intermembral index (~72), whereas for *Pan* (103–106), *Gorilla* (~115), and *Pongo* (~139) it is far higher, reflecting their relatively shorter lower limbs and longer upper limbs. The longer lower limb in humans directly facilitates a longer stride length.

Table 1 Some of the important anatomical features specifically related to bipedal locomotion in modern humans. Some descriptions adapted from Aiello and Dean (1990)

Trait	*Homo sapiens*	African apes	Functional significance in *H. sapiens*
Foramen magnum orientation	Perpendicular to orbital plane	More vertically inclined	Related to vertical positioning of spine
Shape of spine	S curve with lumbar lordosis	C curve with no lumbar lordosis	More efficient balance and support of upright trunk
Intermembral index	Low (~72)	High (103–115)	Longer stride lengths
Size of vertebral bodies	Larger, especially L1-5	Smaller	Increased load of vertical trunk
Shape of iliac blades	Short, wide, and curved	Long, narrow, and flat	Support for vertical trunk
Orientation of iliac blades	Mediolaterally	Anteroposteriorly	Support for vertical trunk
Relative distance from hip to sacroiliac joints	Small	Large	More efficient transfer of weight from spine to hip
Size of acetabulum	Large	Small	Increase in weight transfer through hip joint
Anterior inferior iliac spine (AIIS)	Present	Absent/weak	Attachment site for strong iliofemoral ligament – helps maintain balance by preventing hyperextension of thigh
Femoral head size	Large	Small	Increase in weight transfer through hip joint
Cortical bone distribution in femoral neck	Thicker inferiorly	Even all around	Increase in weight transfer through hip joint
Bicondylar angle of femur	Valgus	Absent/varus	Placement of lower leg closer to midline of body
Relative lengths of articular surfaces of femoral condyles	Similar in length	Lateral condyle shorter	Aids medial rotation of femur and locking of knee joint at heel-strike
Inclination of tibial trochlear surface	Perpendicular to long axis of tibia	More laterally inclined	Allows perpendicular passage of leg over foot
Plantar tuberosity on calcaneus	Two	One	Facilitates stable heel-strike
Longitudinal arches in foot	Two present – one medial and one lateral	Absent	Acts as "shock absorber" and maintains structural rigidity in foot throughout stance phase
Hallux opposability	Absent	Present	Facilitation of efficient toe-off and loss of arboreal grasp
Relative tarsus length	Long	Short	Increases power arm length in foot – leads to more efficient leverage in foot

(*continued*)

Table 1 (continued)

Trait	*Homo sapiens*	African apes	Functional significance in *H. sapiens*
Relative lengths of rays II–V	Short	Long	Decreases level arm length in foot – leads to more efficient leverage in foot
Metatarsal robusticity pattern	1 > 5 > 4 > 3 > 2	1 > 3 > 2 > 4 > 5	Reflects increased transfer of weight along lateral edge of foot
Phalangeal curvature	Flat	Curved	Loss of arboreal grasp

The modern human pelvis is very different in shape to that of all other primates, including the great apes. The iliac blades are short and wide, the ischium extends posteriorly, and the sacrum is relatively wide. These features greatly facilitate support of the upright trunk, place the trunk's center of gravity closer to the hip joint, and allow the lesser gluteal muscles to be positioned at the side of the pelvis (Napier 1967; Rose 1984; Aiello and Dean 1990). This last feature is important, as contraction of these muscles during walking tilts the trunk toward the leg in contact with the ground, providing greater stability and balance. Humans also have a large acetabulum to accommodate a large femoral head, reflecting the relative increase in body weight passing through the hip during locomotion. The modern human femur has a valgus bicondylar angle, resulting in the knee being situated far closer to the midline of the body than the femoral head is. This greatly reduces the lateral deviation of body weight during walking and is argued by many to be an important feature related to habitual bipedal locomotion. However, modern humans who are unable to walk from birth do not develop a valgus bicondylar angle (Tardieu and Trinkaus 1994), and so this trait is best considered as ontogenetic even though its presence indicates habitual bipedal behavior.

The human knee has the unique ability to lock when in full extension, which greatly facilitates upright walking by keeping the leg straight and enabling the efficient downward passage of the body's weight through to the ankle. This locking action is facilitated in humans by having long femoral condyles that are the same length as each other (in *Pan* they are shorter, and lateral condyle is shorter than the medial) and different femoral attachment sites for the posterior cruciate ligament (Aiello and Dean 1990). The distal tibia has a particularly important feature linked to bipedal locomotion worth noting. The talar articular surface is orientated perpendicular to the long axis of the bone, resulting in a less arcuate passage of the leg over the foot (Latimer et al. 1987). This allows more efficient weight transfer through to the foot. The modern human foot is particularly specialized for the requirements of bipedal locomotion. The African ape foot can be considered a grasping organ with some terrestrial adaptations, whereas that of humans is essentially a propulsive platform. Modern humans are the only living primates to have lost the ability to oppose the hallux, which is in line with the remaining toes. Human toes are relatively short and straight, and the tarsus relatively long, with an elongated calcaneal tuberosity. This allows for a more efficient lever-arm to power-arm ratio, which facilitates efficient propulsion during the stance phase. A combination of bony architecture and strong plantar ligaments results in the human foot being arched longitudinally on both the medial and lateral sides. By comparison the ape foot is weight-bearing through the midfoot, and this is reflected in the enlarged medial tuberosity on the navicular. This longitudinal arching combined with strong plantar ligaments and the unique locking morphology of the calcaneocuboid joint allows the human foot to not only act as an efficient shock absorber but also stay rigid during weight transfer to the ground.

Fossil Evidence

The precise number and nature of derived traits characterizing stem hominins is increasingly difficult to determine and likely to remain so. It has recently been pointed out that, in its entirety, bipedality requires a combination of many complex anatomical traits and so cannot necessarily be classed as a dichotomous character (Haile-Selassie et al. 2004). However, it is reasonable to assume that strong evidence of bipedal locomotion is key in determining whether fossil material warrants inclusion within the hominin clade. Perhaps the best way to consider such evidence is to ask whether fossil hominin material indicates *habitual* or *obligate* bipedalism, rather than merely *occasional* bipedalism, which we see in most extant species of great apes (see Rose 1991). Clear evidence of a shift from occasional to habitual bipedalism is important when considering early hominin remains, as is the shift from habitual to obligate bipedalism when considering later hominin remains. In that context, when considering the hominin fossil record, this chapter will consider *occasional* bipeds as those animals with a bipedal component of their locomotor repertoire similar to that of modern-day chimpanzees. By contrast, *habitual* bipeds are considered those taxa that had a significantly increased bipedal component but were by no means exclusively bipedal and would have retained an arboreal component to their locomotor repertoire. *Obligate* bipeds are taxa that were exclusively bipedal and had lost all other forms of terrestrial and arboreal locomotor behaviors.

Precursors of Bipedalism

There is a significant literature on the likely locomotor mode that directly preceded hominin bipedalism (see reviews by Richmond et al. 2001; Harcourt-Smith and Aiello 2004). Early models, in the absence of fossil evidence, relied heavily on observed extant primate locomotor behaviors and phylogenetic hypotheses. Arguably, the prevailing view was that a brachiating, hylobatid-like ancestor evolved into a larger-bodied African apelike ancestor capable of orthograde climbing and terrestrial knuckle-walking, which in turn evolved into a bipedal hominin (e.g. Keith 1903, 1923; Gregory 1916, 1928; Morton 1924, 1935). Minor variants of these models existed between authors, with Morton (1924, 1935) arguing for a more terrestrial "gorilloid" prehuman locomotor mode, while Gregory (1916, 1927) and Keith (1903, 1923) favored a more "troglodytian" hominin precursor. Others argued for a very deep tarsoid ancestry for humans and bipedalism (Wood Jones 1916, 1929) or an arboreal quadruped ancestry of monkey-like above-branch locomotion (Straus 1949).

Despite the elegance of some of these early models, the central factor in understanding the evolution of bipedalism lies in the reconstruction of Late Miocene large hominoid locomotor behaviors. The advent of fossil evidence and molecular dating methods has effectively precluded some of these early theories from being likely. Based on molecular data, the last common ancestor of modern humans and chimpanzees is likely to have lived between 5 and 9 Ma (Gagneux and Varki 2000; Page and Goodman 2001; Springer et al. 2012; Steiper and Seiffert 2012; Schrago and Voloch 2013), and most Miocene hominoid remains do not show a strong adaptation to brachiation (e.g., Napier and Davis 1959; Avis 1962; Rose 1991; Moyà-Solà and Köhler 1996), although the hylobatian model is still argued by some (Tuttle 1974, 1975, 1981). In place of these earlier theories, a number of alternatives can be found in the recent literature. Perhaps the best-known recent theory today is the suggested knuckle-walking ancestry for hominins (Washburn 1967; Richmond and Strait 2000; Richmond et al. 2001), which draws heavily on the specialized knuckle-walking behavior of chimpanzees and gorillas as a model and argues for a retention of traits associated with knuckle-walking in the wrists of *Au. afarensis* and *A. anamensis* (Richmond and Strait 2000). However, this theory is also disputed by others on both paleontological and neontological grounds (e.g., Tuttle and Basmajian 1974; Dainton 2001; Lovejoy et al. 2001; Kivell and Schmitt 2009). While certain Middle and Late Miocene hominoid remains show an increased capacity for terrestriality, no large fossil hominoid taxa from this time-range show adaptations for knuckle-walking behavior (Stringer and Andrews 2005). Recent work on extant primates has also shown that several traditionally accepted knuckle-walking features are not always found in *Pan* and *Gorilla* and that both genera may knuckle-walk in biomechanically distinct ways (Kivell and Schmitt 2009). This leads to the possibility that knuckle-walking may have evolved independently within hominines, although Williams (2010) argues that this may have been unlikely due to the lack of highly integrated knuckle-walking morphologies in *Pan* and *Gorilla*.

Alternate contemporary theories include those suggesting an arboreal climbing ancestor (either large bodied or small bodied) (e.g., Fleagle et al. 1981; Tuttle and Basmajian 1974; Tuttle 1975, 1981; Stern 1975; Prost 1980; Hunt 1996), a terrestrial quadruped ancestor (Gebo 1992, 1996; Sarmiento 1994, 1998), a *Pongo*-like pronograde clambering ancestor (Crompton et al. 2003; Thorpe and Crompton 2005; Thorpe et al. 2007), and even an ancestor that practiced a type of terrestrial "tripedalism" with one limb always free to carry objects (Kelly 2001).

A universal theme that links both the older and the more recent hypotheses is the choice of a single specific locomotor mode as the dominant "precursor" to hominin bipedalism. As Rose (1991) points out, most primates apart from humans usually use several different types of locomotor activity as part of their daily locomotor repertoire. Within the hominoid clade, *Pongo* and particularly *Hylobates* are traditionally considered rather derived and specialized in their locomotor behavior, while *Pan* and *Gorilla* are considered more generalized. However, the great specialization of *Pan* and *Gorilla* in fact lies in that they have a particularly mosaic and versatile locomotor repertoire, especially in the case of the smaller-bodied *Pan*. Both genera regularly engage in terrestrial knuckle-walking, occasional bipedalism, vertical climbing, and orthograde clambering as part of their daily activities. It is quite possible that some of these behaviors, for instance, knuckle-walking, may have been independently acquired in *Pan* and *Gorilla* (e.g., Begun 2004; Kivell and Schmitt 2009). Their locomotor behavior and associated anatomy, however, combined with our current knowledge of the Middle to Late Miocene fossil record, suggest that the immediate precursors to the very first hominins are likely to have been rather generalized hominoids (McHenry 2002) capable of a suite of different locomotor behaviors, although perhaps with an emphasis on arboreal, predominantly orthograde locomotion (Almécija et al. 2013). In that context, it is perhaps rather limited to single out one particular locomotor mode as the likely "precursor" to habitual hominin bipedalism.

Evidence for Habitual Bipedalism Outside the Hominin Clade

Although there is little current evidence to suggest that fossil hominoid taxa existing prior to the Hominini–Panini split had any significant degree of bipedalism in their locomotor repertoires, the possible locomotor affinities of one specific taxon are worth noting. There has been the suggestion that the late Miocene European hominoid, *Oreopithecus bambolii*, was partially bipedal (e.g., Straus 1957, 1962; Kummer 1965; Hürzeler 1968; Köhler and Moyà Solà 1997; Rook et al. 1999). However, that assertion remains highly controversial. Although the iliac blades of *Oreopithecus* are reduced in length, it also has a suite of postcranial features that indicate adaptations to vertical climbing and forelimb suspension, including longer forelimbs than hindlimbs, a flexible shoulder joint, a strong grasping foot, and a lumbosacral region that is incompatible with bipedality (Harrison 1987, 1991; Russo and Shapiro 2013).

Earliest Hominin Evidence

The earliest fossil evidence for potential hominin bipedalism comes from recently discovered Late Miocene cranial remains from Chad, dated to almost 7 Ma and assigned to *Sahelanthropus tchadensis* (Brunet et al. 2002). Virtual reconstruction of the distorted TM266 cranium is argued to show a foramen magnum that is more anteriorly positioned than in *Pan* and *Gorilla* and, more importantly, orientated almost perpendicular to the orbital plane (Zollikofer et al. 2005). This is a trait shared by modern humans and australopiths and indicates a more vertically orientated spinal column that is associated with bipedal locomotion. Currently there are no known postcranial remains of *S. tchadensis*, precluding any further speculation on its locomotor behavior.

Fossil remains from the Lukeino formation in Kenya currently assigned to the putative hominin taxon *Orrorin tugenensis* (Senut et al. 2001) are also argued to indicate bipedality. The material is dated to between 5.7 and 6 Ma (Pickford and Senut 2001; Sawada et al. 2002), and it is reported that there are anatomical features on the BAR 1002’00 proximal femur that indicate habitual bipedal locomotion. The cortical bone of the inferior section of the femoral neck is argued to be relatively thick, and there is an “intertrochanteric groove” for the tendon of the *obturator externus* muscle on the posterior surface (Pickford et al. 2002; Galik et al. 2004). Thick cortical bone on the inferior section of the femoral neck is argued by some to imply habitual bipedalism (e.g., Pauwels 1980; Lovejoy 1988; Ohman et al. 1997), but others have noted that similar patterns of cortical distribution are found in many other primate species and that only apes and atelines differ in having relatively even distribution around the whole neck (Stern and Susman 1991; Rafferty 1998; Stern 2000). There is also debate as to whether the presence of the *obturator externus* tendon groove is reliable in inferring bipedalism. This feature, originally described by Day (1969), is argued to imply regular full extension of the thigh during bipedal locomotion (Day 1969; Robinson 1972; Lovejoy 1978). Others argue that it is not a diagnostic trait of habitual bipedalism (e.g., Stern and Susman 1991) and that it can even be found in quadrupedal cercopithecoids (Bacon 1997). Most recently Lovejoy et al. (2002) posit that while the trait is completely absent in large samples of *Pan* and *Gorilla* and present in australopiths and 60 % of modern humans, it does not specifically imply bipedality, but merely habitual extension of the femur. Despite these somewhat contradictory lines of evidence, more recent metrical analyses of BAR 1002’00 (Richmond and Jungers 2008; Almécija et al. 2013) seem to confirm its hominin status. These studies have found that the femur is strikingly similar to that of later australopiths such as *Au. afarensis*, indicating that *Orrorin* was well adapted to habitual (but not obligate) bipedalism. However, it is also clear that this taxon retained adaptations consistent with arboreality. The upper limb of *O. tugenensis* includes a curved proximal manual phalanx and a humeral shaft with a straight lateral crest for *m. brachioradialis* (Senut et al. 2001; Richmond and Jungers 2008), which are both seen as adaptations reflecting arboreal locomotor behavior (Senut 1981a, b, 1989; Stern and Susman 1983, 1991).

The best-known hominin remains from the Late Miocene/Early Pliocene that indicate bipedalism belong to the genus *Ardipithecus*, from the Middle Awash region of Ethiopia (White et al. 1994, 1995; White 2002). The oldest *Ardipithecus* remains (5.6–5.8 Ma) are ascribed to *Ar. kadabba* and include one proximal fourth pedal phalanx that is described as having strong plantar curvature, but also a dorsally inclined proximal articular surface similar to that of *Au. afarensis* (Haile-Selassie et al. 2004). This latter trait is argued to show that *Au. afarensis* could dorsiflex its foot in a similar way to modern humans (Latimer and Lovejoy 1990b). However, it has also been argued that this feature in *Au. afarensis* is intermediate between modern humans and great apes (Duncan et al. 1994). Until more postcranial remains of *Ar. kadabba* are discovered, its locomotor affinities should be treated with some caution (Haile-Selassie 2001).

The 4.4 Ma *Ardipithecus ramidus* remains are, however, far more comprehensive. Based on a partial cranial base, this taxon was originally reported to have had an anteriorly positioned foramen magnum (White et al. 1994). Following the 2009 announcement of a partial *Ar. ramidus* skeleton (ARA-VP-6/500) with associated cranial and postcranial remains (White et al. 2009), this finding has been confirmed by several studies (Suwa et al. 2009; Kimbel et al. 2014). The rest of the skeleton possesses traits associated with both bipedalism and arboreal locomotor behaviors. The best evidence for bipedality rests with the pelvis. Although the original fossil is damaged and distorted, there is a prominent anterior inferior iliac spine (AIIS), and computerized reconstruction of the iliac blades suggests that they are mediolaterally flared (Lovejoy et al. 2009d). These are features found in later australopiths and indicate bipedality. However, other aspects of the pelvis are more African apelike (such as the elongated superior ischial ramus), and there is no sacrum preserved. In contrast, the relatively long upper limb of *Ar. ramidus* is well adapted for arboreality (Lovejoy et al. 2009b), with curved manual phalanges and a more palmarly orientated capitate head. It is important to note that the hand and wrist of ARA-VP-6/500 do not have any knuckle-walking features (Lovejoy et al. 2009b). The foot also indicates arboreality, as it has a markedly convex and abducted hallucial articular surface on the medial cuneiform, indicating a grasping hallux. Conversely, it is argued that the rather wide lateral side of the cuboid implies the presence of an *os peroneum*, a small sesamoid bone indicative of a powerful *fibularis longus* muscle that would have helped stiffen the lateral foot during the stance phase of upright walking (Lovejoy et al. 2009a).

In a summary paper Lovejoy and colleagues (2009c) have interpreted *Ar. ramidus* as having had a locomotor repertoire made up of bipedalism on the ground and a combination of careful climbing and above-branch, pronograde quadrupedalism when in the trees. Orthograde suspensory behaviors and terrestrial knuckle-walking were definitively ruled out, and the arboreal locomotor component was argued to be somewhat similar to that suggested for the Early Miocene stem hominoid, *Proconsul* (Lovejoy et al. 2009c). It should be noticed that the hominin status of *Ar. ramidus* and its bipedality have been challenged (Harrison 2010; Sarmiento 2010; Wood and Harrison 2011) on the basis that some of the derived features reported in the taxon are found in several, non-bipedal Miocene hominoids. This has been challenged by White and colleagues, who argue that given the particular combination of features found in *Ar. ramidus*, the most parsimonious approach is to class it as a bipedal hominin (White et al. 2010). A preliminary morphometric analysis of the *Ar. ramidus* reconstructed innominate confirms the original suggestion of a derived pelvis partially adapted to bipedality, but also suggests that, when in the trees, *Ar. ramidus* was likely more similar to orthograde suspensory apes such as *Pan* and *Gorilla* (Webb et al. 2013).

In summary, the rather fragmentary fossil record for early hominins allows a degree of speculation as to how bipedal these taxa were. The horizontal orientation of the *Sahelanthropus tchadensis* foramen magnum does certainly indicate that this taxon was likely to have spent more time engaging in bipedal behaviors than either *Pan* or *Gorilla* do, but only the discovery of postcranial remains will further strengthen this argument. The femur of *O. tugenensis* indicates that it was also likely to have been a biped, but its upper limb implies strong climbing. The comparatively extensive remains of *Ardipithecus ramidus* undoubtedly provide the best insight into the locomotion of early hominins and indicate an animal with a pelvis partially adapted to bipedalism, but a foot and upper limb clearly adapted to arboreal climbing behaviors.

The First Habitual Bipeds

Perhaps the first concrete evidence for habitual bipedalism comes with the earliest *Australopithecus* remains from the Kanapoi and Alia Bay localities at Lake Turkana, Kenya. Assigned to *Au. anamensis*, the remains include a large and well-preserved distal and proximal tibia of one individual and are dated to between 3.9 and 4.2 Ma (Leakey et al. 1995, 1998). Crucially, the distal end of the tibia has a horizontal talar surface relative to the long axis of the shaft, implying that the *Au. anamensis* knee would have passed directly over the foot, as in later hominins and modern humans (Ward et al. 1999, 2001). In *Pan* and *Gorilla*, the talar surface is sharply inclined, which results in the knee passing over the foot more laterally during plantigrade locomotion (Latimer et al. 1987).

There are significant australopith postcranial fossil remains from the site of Woranso-Mille, Ethiopia, that at 3.8–3.6 Ma are just slightly younger than the youngest *Au. anamensis* specimens. They include a partial skeleton with an almost complete scapula, a partial pelvis, ribs, and well-preserved upper and lower limb bones. Overall, these remains are argued to strongly imply committed bipedalism with little in the way of arboreal specialties (Haile-Selassie et al. 2010). As they are currently assigned to *Au. afarensis*, see section “Locomotion in Australopiths” for more discussion concerning this taxon.

Following the *Au. anamensis* and Woranso-Mille remains the, record becomes richer and starts with what is arguably one of the best-known and strongest lines of evidence for early hominin bipedalism: the Laetoli footprint trail. Laetoli, Tanzania, is the type locality for *Au. afarensis* (see below) and has produced a number of hominin fossils assigned to this taxon. However, it is perhaps best known for its extraordinary series of preserved animal tracks, first discovered in 1976. Excavation through 1977–1979 revealed at least two (and probably three) trails of unmistakably bipedal hominin footprints preserved in a volcanic ash-fall layer that had become wet from rainfall (Leakey and Hay 1979; Leakey and Harris 1987; White and Suwa 1987). The footprints are dated between 3.5 and 3.7 Ma (Hay and Leakey 1982; Drake and Curtis 1987). The most distinctly hominid tracks are those from Site G, where there are two trails (and a possible third overprinted on the larger G-2 tracks). There is also a putative hominin track at Site A, but that has been argued by Tuttle et al. (see 1991) to have probably belonged to an ursid.

Most researchers agree that the G-1 and G-2 series of tracks are very humanlike, with no evidence of any type of forelimb support. The best preserved prints show a strong heel-strike and toe-off and indicate a transmission of body weight through the stance phase of walking similar to that of modern humans. In accordance with this, there is evidence of longitudinal arching, and the hallux is in line with the remaining toes (Day and Wickens 1980; Robbins 1987; Tuttle 1987; White and Suwa 1987). Stern and Susman (1983) do argue that the footprints show a "transitional" morphology between apes and modern humans, but the prevailing view remains that they are very humanlike. Schmid (2004) has argued that although the prints were made by habitual bipeds, there is some evidence of increased rotational movement of the upper body reflecting a more apelike morphology of the trunk. This in turn implies an "ambling" gait-pattern inconsistent with the ability to run. More recent analyses of the prints using three-dimensional analytical techniques (e.g., Raichlen et al. 2010) have confirmed that the Laetoli hominins had a very humanlike weight transfer pattern during walking.

There is much more debate over the taxonomic assignation of these trails. Most researchers accept that *Au. afarensis* is likely to have made them, given that the type specimen for that taxon comes from Laetoli and is roughly contemporary with the footprints. Others, principally (Tuttle 1981, 1987; Tuttle and colleagues 1990, 1991), have argued that the prints are so humanlike that they are incompatible with the known *Au. afarensis* remains from Hadar, which have long and curved pedal phalanges. They argue that another, as yet undiscovered, hominin must have made the tracks, which would have had feet far more humanlike than the Hadar *Au. afarensis* specimens. White and Suwa (1987) addressed this issue with a large study in which they reconstructed a hypothetical *Au. afarensis* foot using an amalgam of Hadar bones and the *Homo habilis* foot complex from Olduvai, OH 8 (Day and Wood 1968). They argued that this reconstruction perfectly matched the Site G footprints. However, at 1.76 Ma, OH 8 is almost 2 younger million years than the Laetoli trails and has a very different combination of morphologies to the Hadar remains (Day and Napier 1964; Kidd et al. 1996; Harcourt-Smith 2002), while a number of studies have shown that the Hadar *Au. afarensis* are unlikely to have had longitudinal arching in the foot, as seen in the Laetoli prints (Berillon 2000, 2003; Harcourt-Smith 2002; Harcourt-Smith and Hilton 2005; DeSilva and Throckmorton 2010). There are also a number of Hadar tarsal remains, including calcanei, two naviculars, and two tali that would be better suited to making a reconstruction of the *Au. afarensis* foot. Despite all this debate, what is certain is that the footprints provide an excellent temporal benchmark in terms of the origins of bipedalism. They mark a distinct behavioral event in time, which fossils can never do. In that context we can be sure that at least one line of hominins were practicing habitual bipedalism by at least 3.6 Ma, which implies that the shift from occasional to habitual bipedalism occurred sometime well before that and probably well before 4 Ma.

Locomotion in Australopiths

There has probably been more debate over the locomotor affinities of members of the genus *Australopithecus* than over any other taxa. This is partially due to the fact that there is a relatively rich postcranial record for this genus. However, the main reason is that these remains show intriguing combinations of primitive and derived traits relating to both terrestrial and arboreal locomotor behaviors. Historically the South African *Au. africanus* remains provided the major focus of work through to the early 1970s, perhaps culminating in Robinson's seminal treatise "Early Hominid Posture and Locomotion" in 1972. Between the 1970s and the 1990s, the discovery in Ethiopia of extensive postcranial remains assigned to *Au. afarensis*, including the famous "Lucy" skeleton, has shifted the debate to East Africa and back as far as 3.4 Ma. The *Au. afarensis* remains are considerably older than those of *Au. africanus* and along with Laetoli confirm that bipedal locomotion was likely to have been selected for well before brain expansion and tool-making behavior. Most recently the exciting new *Au. sediba* remains from South Africa have considerably added to the locomotor variation we see within the genus. In this section we will review the morphology and associated locomotor behavior of *Au. afarensis*, *Au. africanus*, and *Au. sediba* in turn.

Au. afarensis

This taxon provides the first direct anatomical evidence of a true shift from occasional to habitual bipedalism. However, there has been much disagreement over the precise locomotor affinities of this taxon, most of which falls into two distinct camps. Some researchers argue that *Au. afarensis* was almost as proficient a biped as modern humans (e.g. Latimer 1991; Lovejoy et al. 2002; Ward 2002). Others argue that in fact this taxon had a significant number of primitive postcranial traits that must have implied an important arboreal component to its locomotor repertoire (e.g., Susman et al. 1984; Stern 2000). These views are rather polarized, and it is best to consider *Au. afarensis* as highly mosaic in its adaptations (see McHenry 1991, for a comprehensive review of primitive and derived traits in the Hadar hominins).

The first specimen of *Au. afarensis* to be discovered showing evidence for bipedality was the AL 129 knee, discovered at Hadar, Ethiopia, and consisting of a well-preserved distal femur and associated proximal tibia (Taieb et al. 1974). Crucially, the morphology of the distal femur indicated a bicondylar angle even higher than that of modern humans (Johanson et al. 1976). This implied that the leg of *Au. afarensis* would have passed close to the midline of the body as in humans, which is an important adaptation to bipedal locomotion. Subsequent discoveries at Hadar, including the AL 288 partial skeleton ("Lucy") and the extensive AL 333 assemblage, provided further evidence of a strong selection for bipedality. The AL 288 skeleton, approximately 40 % complete, included a well-preserved pelvis, ribs, vertebrae, and representative pieces of all major limb elements. In overall morphology, the pelvis of "Lucy" is far more similar to that of modern humans. The iliac blades are short and wide, which would have allowed the lesser gluteal muscles to be situated laterally and act as pelvic abductors. The wide sacrum, situated behind the hip joint, would also have kept the center of mass of the trunk close to the hip, allowing efficient transfer of the weight to the lower limb during walking. Finally, there is a prominent anterior inferior iliac spine, indicating the importance of the knee extensor, *rectus femoris*, and a strong attachment for the iliofemoral ligament which helps maintain balance by preventing hyperextension of the thigh (Aiello and Dean 1990). It is worth noting that the pelvis of AL 288 is also unique in being markedly wide, more so than in modern humans, and that its iliac blades are not orientated as anteriorly–posteriorly as they are in humans. This considerable width may well be functionally linked to the more funnel-shaped rib cage of *Au. afarensis* (Schmid 1983, 1991). Such a rib cage would have been relatively wider inferiorly than in humans, therefore requiring a wider pelvis to support the resulting wider trunk. However, overall the anatomy of the *Au. afarensis* pelvis implies that it was well suited to two of the major requirements of bipedalism: maintaining balance and efficiently transferring weight from the trunk to the leg during walking.

Apart from the high bicondylar angle in *Au. afarensis*, it has been argued that its long femoral neck is especially adapted to bipedality. This feature may in fact have made abduction of the hip biomechanically easier than in modern humans (Lovejoy 1973; Lovejoy et al. 1973). However, it is also possible that this feature is a reflection of the wider thorax and pelvis in *Au. afarensis*. There are a number of other traits in the lower limb that unequivocally imply habitual bipedality. The mediolateral orientation of the talar surface of the distal tibia is horizontal relative to the long axis of the shaft. As discussed in section “Associated Anatomical Differences Between Humans and Great Apes,” this is an important feature unique to later bipedal hominins that facilitates efficient transfer of weight from the leg to the foot. In the *Au. afarensis* foot, the talus is very humanlike, particularly with respect to the trochlear surface (Latimer et al. 1987). The calcaneus has a lateral plantar process on the tuberosity, which greatly helps dissipate stress produced by ground reaction forces at heel-strike (Latimer and Lovejoy 1989). In general the morphology of the ankle joint and heel in *Au. afarensis* is extremely humanlike and would have been well suited to coping with the increased forces through the ankle associated with bipedal locomotion. It is also argued that the *Au. afarensis* foot would not have been capable of opposing its hallux (Latimer and Lovejoy 1990a).

Other features present in the postcranium suggest bipedalism, but are more open to interpretation. The femoral neck in both the AL 128–1 and Maka femora has thicker cortical bone inferiorly than superiorly (Lovejoy et al. 2002). As discussed in section “Earliest Hominin Evidence,” there is disagreement concerning this trait being used to confidently imply bipedality. The femoral condyles of larger-bodied members of *Au. afarensis* are also more humanlike in proportions and symmetry, but this is not the case for smaller members of the species, such as AL 129 (Aiello and Dean 1990). In the foot, it has been argued that *Au. afarensis* had more dorsally orientated proximal articular facets on the proximal pedal phalanges, implying a human-like ability for increased dorsiflexion of this joint in bipedal walking (Latimer and Lovejoy 1990b). However, a subsequent metrical study found that the *Au. afarensis* angle actually falls well outside the human range of variation and between humans and the African apes (Duncan et al. 1994). The foot of *Au.*

afarensis had also been suggested to have had strong longitudinal arching (e.g., Latimer and Lovejoy 1989; Ward et al. 2011). This assertion is partially related to the assumption that the arched footprints from Laetoli were made by *Au. afarensis*. As discussed in section "The First Habitual Bipeds," this may not be the case, and when assessing the degree of arching in this taxon, it is best to assess the fossil remains directly. The markedly enlarged medial tuberosity on two navicular bones from Hadar strongly implies considerable weight-bearing in the midfoot of *Au. afarensis* (Sarmiento 2000; Harcourt-Smith et al. 2002; Harcourt-Smith and Hilton 2005). Such morphology is incompatible with longitudinal arching. A comprehensive architectural analysis of the *Au. afarensis* pedal material by Berillon (2003) also finds that this taxon was unlikely to have had a longitudinal arch, and recent work linking distal tibial morphology and arch height reached similar conclusions (DeSilva and Throckmorton 2010). However, an analysis of a well-preserved fourth metatarsal from Hadar does argue for a longitudinal arch due to humanlike torsion of the metatarsal head relative to the base (Ward et al. 2011). Drapeau and Harmon (2013) challenge these findings and point out that such torsion can only really inform on the presence of a transverse longitudinal arch, a trait many extant primates possess. They note that cercopithecoids and modern humans have similar levels of torsion for this reason, even though cercopithecoids do not have a longitudinal arch.

There are also a number of more apelike traits in the *Au. afarensis* postcranium, some of which suggest a degree of arboreal climbing ability (see Stern 2000). Most noticeably, the manual and pedal proximal phalanges from the AL 288 and AL 333 localities, as well as from the infant Dikika specimen, are markedly curved and long and have prominent flexor ridges (Marzke 1983; Stern and Susman 1983; Susman et al. 1985; Alemseged et al. 2006). These features strongly imply an arboreal proficiency not found in later hominins. In the foot, the morphology of a partial medial cuneiform bone from AL 333 also implies that there may have been a degree of hallucial opposability (Harcourt-Smith et al. 2003), although others assert this to not be the case (Latimer and Lovejoy 1990a). Elsewhere, it has been reported that that the morphology and function of the *Au. afarensis* calcaneocuboid joint may have been apelike (Gomberg and Latimer 1984). Analysis of the limb proportions of the AL 288 skeleton show that the femur was relatively short (Jungers 1982; Jungers and Stern 1983), meaning that "Lucy" would have had much shorter stride lengths than modern humans. The morphology of the tibial plateau indicates that *Au. afarensis* would have had a single attachment for the lateral meniscus, as in apes (Senut and Tardieu 1985), although the phylogenetic relevance of this trait has recently been questioned (Holliday and Dugan 2003). In the upper limb, it has been argued that the distal humerus of smaller-bodied *Au. afarensis* specimens shows a well-developed lateral trochlear crest, an apelike trait that prevents dislocation of the elbow joint during climbing/suspension (Senut 1981a, b; Senut and Tardieu 1985) and a more cranially orientated glenoid in the scapula (Stern and Susman 1983). Both these features could have facilitated the arm's being used in above-branch climbing behaviors. However, more recent finds have added to the debate over *Au. afarensis* shoulder function. The 3.3 Ma Dikika specimen, a presumed

3-year-old female, has a complete scapula that is most similar to its counterpart in *Gorilla*, something that is argued to imply arboreal locomotor behavior (Alemseged et al. 2006). Conversely, the older Woranso-Mille adult partial skeleton KSD-VP-1/1 (3.8–3.6 Ma) is argued to have a scapula with a combination of *Gorilla*-like and *Homo*-like features, but overall a total morphological pattern that was incompatible with suspensory locomotion (Haile-Selassie et al. 2010). In the wrist it has been suggested that *Au. afarensis* retained features consistent with a knuckle-walking ancestry (Richmond and Strait 2000, although the authors do not go so far as suggest that *Au. afarensis* itself had a capacity for knuckle-walking. Others disagree with this assertion (Dainton 2001; Lovejoy et al. 2001), and it is interesting to note that none of the other important morphological traits associated with knuckle-walking (e.g., transverse dorsal ridges and dorsally expanded articular surfaces on the metacarpal heads) are found in *Au. afarensis* specimens (Stern and Susman 1983).

It has also been suggested that there is a significant degree of postcranial variation between larger-bodied and smaller-bodied individuals of *Au. afarensis*, particularly in the knee and elbow joints as discussed above, but also in the ankle (Stern and Susman 1983; Senut and Tardieu 1985). These differences could imply locomotor differences between the sexes, as Stern and Susman have suggested (1983), but have also been interpreted as suggesting that there were two distinct species of hominin at Hadar (e.g., Senut and Tardieu 1985; Tardieu 1981, 1983, 1986, 1993, 1994; Deloison 1999). However, the prevailing view remains that the Hadar material constitutes a single species (Harcourt-Smith and Aiello 2004), although there continues to be disagreement over the degree of sexual dimorphism in *Au. afarensis* (e.g., Plavcan et al. 2005; *contra* Reno et al. 2003).

The considerable debate over the locomotor behavior of *Au. afarensis* ultimately rests on how one views the evolutionary relationship between these traits and the process of selection (Ward 2002; Harcourt-Smith and Aiello 2004). One can argue, as Latimer (1991) does, that the derived anatomical adaptations to bipedalism seen in *Au. afarensis* demonstrate clear evidence of directional selection toward bipedality. Conversely one can also argue that the retention of primitive apelike traits present in *Au. afarensis* indicates a degree of stabilizing selection for arboreal proficiency (e.g., Stern and Susman 1983; Stern 2000), although there have also been suggestions that such features in *Au. afarensis* were reflective of efficient terrestrial quadrupedalism (Sarmiento 1994, 1998). Only a better understanding of the relationship between many of these traits and ontogenetic and/or epigenetic factors may help to resolve this debate (Lovejoy et al. 2002; Harcourt-Smith and Aiello 2004).

Overall, the postcranial skeleton of *Au. afarensis* can be best considered as mosaic showing a combination of derived humanlike bipedal traits, primitive apelike climbing-related traits, and a number of traits that appear to be unique. There is no doubt that *Au. afarensis* was a habitual biped and would have spent a significant amounts of time engaging in bipedal locomotor behaviors, but there are enough arboreal adaptations present to imply a degree of climbing ability, and it is not unreasonable to suggest that *Au. afarensis* could have spent time in trees at night and for predator avoidance.

The Burtele Remains

In contrast to the extensive remains within the *Au. afarensis* hypodigm, there is one new similarly aged (3.4 Ma) partial foot from the site of Burtele in Ethiopia that appears to have been distinct to that of *Au. afarensis*. Although not yet taxonomically assigned, its discoverers argue that it had strong grasping abilities, with an opposable hallux (Haile-Selassie et al. 2012). The only other hominin with such a feature is *Ar. ramidus*, and the authors suggest that the Burtele hominin was similar to that taxon in its locomotor adaptations. If true this would strongly lend support to the hypothesis that multiple forms of bipedalism existed in different hominin lineages from the Late Miocene through to the Pleistocene (Harcourt-Smith and Aiello 2004). However, three-dimensional metrical analyses of the AL 333–54 hallux from Hadar have shown that it is more apelike than humanlike (Proctor et al. 2008), and further work will be needed on the Burtele foot to ascertain that it is distinct from that *Au. afarensis*.

Au. africanus

Until the discovery of the Hadar remains in the 1970s, the South African *Au. africanus* fossils provided the best insight into the locomotor behavior of ancient fossil hominins. This was initiated by the discovery of the Taung Child in the 1920s and Dart's (1925) description of its foramen magnum as being in a more humanlike position, thus implying upright posture and locomotion. Since then a large number of fossils assigned to *Au. africanus* have been discovered, predominantly from the site of Sterkfontein (Partridge et al. 1999). The most diagnostic specimen of bipedality is the partial skeleton, Sts 14, which includes a partial pelvis and femur and vertebral fragments and has been argued to belong to the same individual as the Sts 5 skull (Thackeray et al. 2002). The pelvis is morphologically very similar to AL 288, in having wide and short iliac blades and being predominantly more humanlike than apelike (McHenry 1986). Also like AL 288, the pelvis of *Au. africanus* is very wide, with laterally flaring iliac blades and a relatively smaller acetabulum and iliosacral joint. This high pelvic width is confirmed by other *Au. africanus* pelvic fragments, including the reconstructed StW 431 pelvis from Member 4, Sterkfontein (Kibii and Clarke 2003). As for *Au. afarensis*, this is argued to have provided a distinct advantage in bipedal walking (Lovejoy 1973). Distal femora from Sterkfontein (TM 1513 and Sts 34) also indicate that *Au. africanus* had a high bicondylar angle, as in *Au. afarensis* and modern humans. More recently discovered *Australopithecus* postcranial remains from the Jacovec Cavern at Sterkfontein, which may be as old as 4.0 Ma, include a proximal femur (Stw 598) that has a markedly long neck and short head, as for the *Paranthropus* femora from Swartkrans (see below) (Partridge et al. 2003).

Other aspects of *Au. africanus* locomotor anatomy have been argued to be more mosaic. Analysis of the relative size of the semicircular canals in the inner ear indicates that *Au. africanus* had canals of apelike proportions. The morphology of the semicircular canals is closely linked to locomotor behavior, and while this finding does not preclude *Au. africanus* from having been a biped, it is likely that it would have been less competent at complex bipedal behaviors such as running and jumping (Spoor et al. 1994). McHenry and Berger (1998a, b) argue, mainly based on analysis of the Stw 431 skeleton, that *Au. africanus* had relatively large upper limbs and small lower limbs, implying a more prominent climbing-related component of its locomotor repertoire. However, Stw 431 does not have any lower limb remains, only a partial pelvis with a preserved acetabulum and sacroiliac joint, and this limits the scope of their study. It is important to note that this study is often misinterpreted as stating that the limb proportions (e.g., humerofemoral index) of *Au. africanus* were primitive. In fact the study mainly concentrated on measurements taken from the articular surfaces at the ends of limb elements. It has also been argued that a proximal tibia from Member 4, Stw 514a, is "chimpanzee like," in having a more rounded lateral profile of the lateral condyle, thus inferring an apelike range of motion at the knee joint (Berger and Tobias 1996). This may have been so, but it is premature to describe a structure as complex as the proximal tibia as apelike based on one feature alone, and further analysis is needed.

Finally, full recovery and analysis of the well-preserved Stw 573 "Little Foot" skeleton from Member 2 (Clarke and Tobias 1995; Clarke 1998) may prove vital in helping to resolve debate surrounding the locomotion of *Au. africanus*. Stw 573 promises to one of the most important discoveries in the early hominin fossil record, as it is far more complete than that of "Lucy," with a complete skull, a scapula, arm and hand bones in articulation, leg bones, foot bones, ribs, and fragments of vertebrae and the pelvis (Clarke 1999, 2002, 2013). The date of Stw 573 has been the subject of considerable debate, ranging from almost 4 to 2.2 Ma, although recent advances in dating methods and a better understanding of the complex stratigraphy of Sterkfontein have resulted in a likely range of 2.6–2.2 Ma (Herries et al. 2013). Most of these bones await removal from the breccia, but the foot bones were found separately and were initially described as showing a mosaic of adaptations, with a partially opposable hallux capable of some grasping potential, but a more humanlike ankle joint (Clarke and Tobias 1995). However, metrical analyses of these remains show that while Little Foot could not have opposed its hallux and had a navicular distinct from those at Hadar, it did have a more apelike ankle joint, implying that overall the foot was mosaic, but in a different way to that originally suggested (Harcourt-Smith 2002; Harcourt-Smith et al. 2003; Harcourt-Smith and Aiello 2004; Kidd and Oxnard 2005; McHenry and Jones 2006). It should be noted that while Stw 573 was originally argued to possibly belong to *Au. africanus* (Clarke and Tobias 1995), it has recently been suggested that it might instead belong to a different species of australopith (Clarke 2013).

Au. sediba

The discovery of the *Au. sediba* associated skeletons from Malapa, South Africa (Berger et al. 2010), has provided a fascinating new twist to the debate surrounding the emergence of obligate bipedalism. Dated to 1.95–1.78 Ma (Berger et al. 2010), *Au. sediba* is contemporary with as many as six different hominin taxa across southern and eastern Africa. When considering the locomotion of *Au. sediba*, analysis of the hand bones implies arboreal locomotor capabilities (Kivell et al. 2011). This is not inconsistent with the predicted locomotor behavior for other, earlier species of *Australopithecus*. However, more surprising information comes from the pelvis and foot. Although some features of the pelvis are shared with other species of *Australopithecus*, it has many more derived, *Homo*-like features than not. The iliac blades are more vertically orientated and have a sinusoidal anterior border, the ischia are shortened, and the distance from the sacroiliac joint to the hip joint is reduced (Kibii et al. 2011). Given that *Au. sediba* has a small, australopith-sized brain, the markedly more human-like pelvis implies a level of anatomical remodeling most likely related to locomotion and challenges the hypothesis that pelvic remodeling in Plio-Pleistocene hominins was related to obstetric constraints related to increased brain size (e.g., Lovejoy et al. 1973).

The foot of *Au. sediba* is, conversely, very mosaic. The ankle joint is humanlike, but the medial malleolus of the tibia is markedly thick mediolaterally, and the calcaneus is primitive in lacking a lateral plantar process, unlike *Au. afarensis* and modern humans (Zipfel et al. 2011). Combined with other features in the lower limb, including a very high lateral patella lip on the distal femur, these pedal features are argued to indicate a form of hyperpronating bipedalism in *Au. sediba* entirely distinct from that of other australopiths (DeSilva et al. 2013), providing further evidence of locomotor diversity in early hominins (Harcourt-Smith and Aiello 2004; McHenry and Brown 2008).

Paranthropus

The majority of available postcranial material from the genus *Paranthropus* come from the South African sites of Swartkrans and Kromdraai and are assigned to *Paranthropus robustus*. There are no complete long bones for *P. robustus*, but from Swartkrans there are a partial pelvis (SK 50), two proximal femora (SK 82 and 97), and a number of other postcrania including hand and foot bones, while from Kromdraai there is a partial talus (TM 1517). Two major studies on this postcranial material, by Napier (1964) and Robinson (1972, 1978), argued that *P. robustus* had a slightly less-derived postcranial skeleton than *Au. africanus* and would have had a less efficient type of bipedal gait. The main anatomical arguments for this were a more laterally facing acetabulum and longer ischium in the SK 50 pelvis, smaller femoral heads, and a more medially orientated talar neck and head, which has been sometimes linked to hallux opposability (Broom and Schepers 1946; Napier 1964; Robinson 1972). However, the SK 50 pelvis is severely distorted, and it is questionable whether there is enough well-preserved morphology for serious anatomical analysis. The Kromdraai talus, although apelike in some metrical aspects (Wood 1974), also has a relatively flat humanlike trochlear surface (Robinson 1972), and the significance of talar neck orientation to grasping potential has been brought into question by Lewis (1980, 1989). More recent finds assigned to *P. robustus* suggest that it was, in fact, likely to have been an efficient biped (Susman 1989). In particular, two well-preserved first metatarsals from Swartkrans show that *P. robustus* would have had a strong toe-off during walking, which is in concordance with efficient bipedality (Susman and Brain 1988; Susman and de Ruiter 2004). There is little in the way of confidently assigned postcranial remains of *P. boisei*, though a recently described partial skeleton from Olduvai Gorge, Tanzania (Domínguez-Rodrigo et al. 2013), indicates that this taxon may have had large, powerful forelimbs.

Locomotor Differences and Similarities Among Australopiths

The postcrania of *Au. afarensis*, *Au. africanus*, and *Au. sediba* all show distinct adaptations for bipedal locomotion. Particularly in *Au. afarensis*, however, there is also strong evidence of retained apelike traits indicating a proficiency for arboreal climbing, especially within the upper limb. There is no doubt that all these taxa were habitual bipeds, but at the same time they cannot be considered as obligate bipeds, and it is best to treat them as having had degrees of mosaicism in their locomotor repertoires. A number of studies have suggested that *Au. africanus* and *Au. afarensis* were very similar to each other in their locomotor anatomy (e.g., McHenry 1986; Dobson 2005). However, a number of other studies show that there are in fact morphologically, and this functionally, distinct. In a major analysis of the Stw 431 skeleton, Haeusler (2001) argues that there are a number of subtle but significant anatomical differences between the Stw 431 and Al 288 pelves implying that *Au. africanus* may have had a more humanlike type of bipedalism. Work on the tarsal bones of australopiths also shows that the putative Stw 573 *Au. africanus* foot may well have been mosaic (see above for details) in a different way to that of *Au. afarensis* (Harcourt-Smith 2002; Harcourt-Smith et al. 2003). Finally, it is clear that *Au. sediba* is distinct from other australopiths, especially concerning its far more humanlike pelvis. Given that *Au. sediba* also retained more primitive features in the foot and upper limb that respectively imply a unique form of bipedalism and possibly arboreality, it seems increasingly likely that from the Early Pliocene through to the Early Pleistocene, there was perhaps a significant degree of locomotor diversity within *Australopithecus*. *Au. afarensis*, *Au. sediba*, and *Au. africanus* all show clear adaptations for bipedality, but it is entirely possible that they were achieved through different evolutionary pathways (Harcourt-Smith and Aiello 2004).

The Rise of Obligate Bipedalism

In section “Locomotion in Australopiths,” I discussed locomotor behavior within the genera *Australopithecus and Paranthropus*. While there may well have been some diversity in the way that different species of *Australopithecus* were bipedal, what is certain is that they cannot be considered as fully obligate bipeds in the way that modern humans are. Conversely, later species of *Homo*, such as *H. erectus*, *H. antecessor*, and *H. neanderthalensis* were unequivocally obligate bipeds (see Fig. 1 for a summary of which taxa there is agreement and disagreement over concerning bipedalism). There are some subtle anatomical differences in the postcranial skeletons of these taxa when compared to modern humans, but their overall skeletal biology strongly implies fully humanlike bipedal locomotion (e.g., Trinkaus 1983; Aiello and Dean 1990; Lorenzo et al. 1999). It seems, then, that the emergence of true obligate bipedal locomotor behavior occurred between about 2.5 and 1.8 Ma. This time period is associated with the emergence of the genus *Homo*, with which the emergence of obligate humanlike bipedalism is likely to prove to be strongly associated.

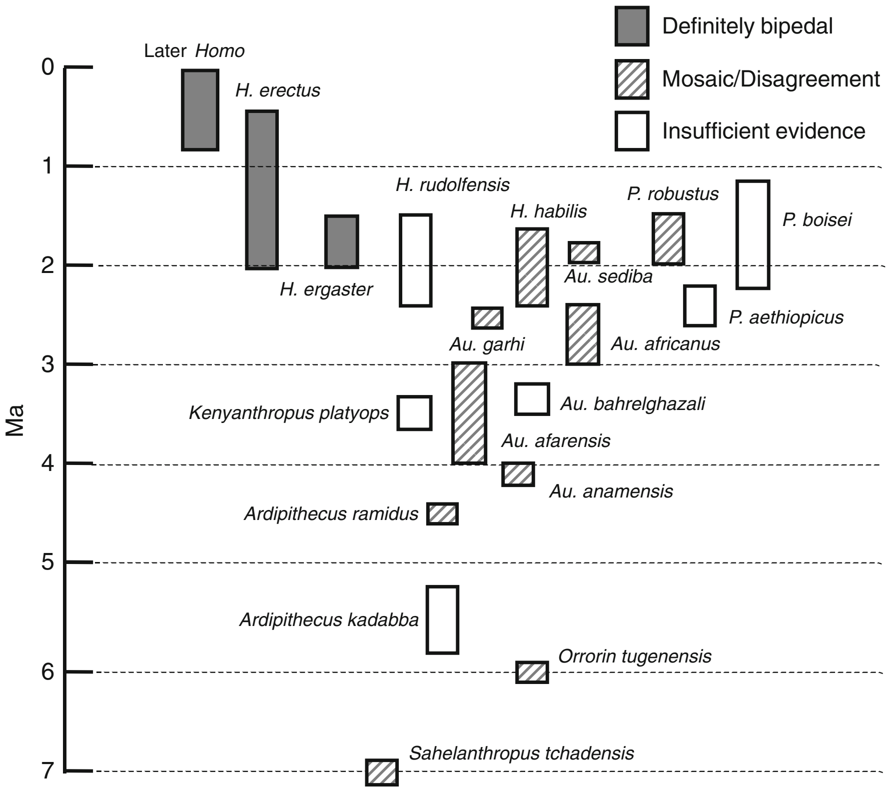

Fig. 1 Temporal ranges of known hominin taxa. Solid shading indicates taxa that were unequivocally obligate bipeds. Cross-hatching indicates taxa where they are mosaic, or there is disagreement over the degree to which they were bipedal. No shading relates to those taxa where there is insufficient evidence (Adapted from Wood (2002))

This period is also extremely complex in terms of hominin evolution and has been the subject of a very diverse range of taxonomic interpretations. At least ten widely accepted hominin species have first or last appearances within this time frame, and the fossil record implies that there was considerable overlap in the temporal and geographical distribution of many of these taxa. Determining which of these species were fully obligate bipeds, and which were not, has been hampered by a number of factors. The principle issue is a meagre postcranial fossil record, but even where there are significant numbers of postcranial elements, as at Koobi Fora (Leakey et al. 1978), there are often problems of reliable taxonomic association. However, the 1.8 Ma juvenile *Homo ergaster* skeleton from Nariokotome, Kenya (KNM-WT 15000), was unequivocally that of a full biped. Its postcranial skeleton is remarkably humanlike, with long legs and short arms and all of the derived postcranial traits associated with obligate bipedal locomotion (Ruff and Walker 1993). With such an advanced body plan, it is reasonable to assume that *H. ergaster* and possibly its direct precursors had developed obligate bipedal behavior before 2 Ma. There are a number of other postcranial remains from Koobi Fora that imply striding bipedalism. In particular the femora KNM-ER 1472 and 1481A are long and extremely humanlike. However, it is difficult to speculate whether these specimens belonged to *H. rudolfensis*, *H. ergaster*, or even *P. boisei*. More recently, 1.5 Ma hominin footprints discovered at Koobi Fora also indicate extremely humanlike bipedalism (Bennett et al. 2009). Study of the prints suggests that they are not only more humanlike than those at Laetoli, (Bennett et al. 2009) but also are compatible with body mass and height estimates for *H. ergaster*. However, as for many other remains at this site, they cannot confidently be assigned to any one taxon.

African Early *Homo*

Most of the debate over the locomotor affinities of early members of *Homo* has concentrated on postcranial remains assigned to *Homo habilis* from Olduvai Gorge, Tanzania. Found at site FLK NN, the holotype for this taxon, OH 7, includes a number of predominantly juvenile hand bones. These bones are argued to be mosaic in their overall morphology. The scaphoid is apelike, the proximal and intermediate phalanges are more curved than in modern humans, and the intermediate phalanges have more apelike attachments for *m. flexor digitorum superficialis*, a muscle associated with climbing and suspensory behavior (Susman and Creel 1979; Aiello and Dean 1990). The OH 8 foot, also found at FLK NN, is included as a paratype of *H. habilis* and provides the best insight into the locomotor behavior of this taxon (Day and Napier 1964; Leakey et al. 1964). Extensive analyses of these bones indicate that the foot had strong longitudinal arches, a locking calcaneocuboid joint, a metatarsal robusticity pattern similar to that of modern humans, and perhaps most importantly a hallux in line with the remaining toes that was wholly incapable of any opposability (Day and Napier 1964; Susman and Stern 1982; Berillon 1999, 2000; Harcourt-Smith and Aiello 1999). The combination of all these features points to an individual capable of efficient bipedal locomotion. However, the talus is less humanlike than the remaining foot and has a trochlea that is strongly grooved and medially sloping. This is a more-apelike morphology and is consistent more laterally arcuate passage of the leg over the foot during the stance phase (Latimer et al. 1987). The implication of this is that although the OH 8 foot is very humanlike in most critical features, its ankle joint implies less efficient weight transfer from the leg during walking. There are also the OH 35 distal tibia and fibula, which were found at site FLK (Davis 1964). These are argued to be humanlike, with a talar facet that is perpendicular to the long axis of the shaft and predominantly humanlike muscle attachments (Davis 1964; Lovejoy 1975; Susman and Stern 1982). It has been argued that OH 35 is likely to have come from the same individual as OH 8 based on morphological similarity (Susman and Stern 1982). Recent metrical comparisons contradict that assertion (Aiello et al. 1998), and it should be noted the two specimens were found 300 yards apart and in different geological horizons (Davis 1964; Dunsworth and Walker 2002).

The other specimen of interest from Olduvai is the more recently discovered partial skeleton OH 62, found at site FLK and assigned to *H. habilis* based on associated craniodental remains (Johanson et al. 1987). Although OH 62 is extremely fragmentary, it has been argued that the intermembral proportions were more apelike and similar to that of *Au. afarensis*. This assertion was based on humerofemoral proportions that relied on the femoral length of OH 62 being estimated as similar to those of the considerably older *Au. afarensis* AL 288 (Johanson et al. 1987; Hartwig-Scherer and Martin 1991). Based on these findings, it has also been suggested that OH 62 has limb proportions as primitive as those of *Au. africanus* (McHenry and Berger 1998a, b). However, the OH 62 femur is incomplete, lacking a considerable part the distal end, and it is impossible to accurately estimate the correct length of this fossil (Korey 1990; Haeusler and McHenry 2004). Furthermore, an alternative reconstruction of the OH 62 femoral length, based on morphological similarity to the younger (1.15–0.8 Ma) and undescribed OH 34 femur from Bed III, yields a far more humanlike value, indicating more humanlike limb proportions (Haeusler and McHenry 2004). Given that OH 34 may have been subjected to a degree of post-depositional erosion that may have compromised its morphology (Day and Molleson 1976), this latter finding must also be treated with caution. However, given that the OH 35 tibia and fibula are also relatively long, it is not unreasonable to assume that the limb proportions of *H. habilis* could have been rather more humanlike than some have suggested. Until further material is uncovered, the evidence is not strong enough to be definitively sure of either scenario. More recently Ruff (2009) has addressed the cross-sectional properties of the OH 62 long bones and concluded that the humeral and femoral strength proportions were outside the modern human range of variation and within that of *Pan*, implying that *H. habilis* was not an obligate biped and retained some arboreal specializations.

There are thus a number of things that can and cannot be said about the locomotor affinities of *H. habilis*. The foot, tibia, and fibula are all very humanlike in most critical aspects. There is some degree of uncertainty concerning whether the limb proportions were more human or apelike, but this issue cannot be currently resolved. The hand bones show a mosaic of humanlike and apelike morphologies that may imply some climbing activity, and this is supported by analyses of the cross-sectional properties of the long bones. Therefore, a conservative estimation of the locomotor behavior of *H. habilis* would place it *between* the habitual bipedalism of the australopiths and the obligate bipedalism of *H. ergaster* and later species of *Homo*. The ambiguity surrounding the locomotor affinities of *H. habilis* has been used by some to add weight to the argument that it should be transferred to the genus *Australopithecus* (e.g., Wood and Collard 1999). There may or may not be the case craniodentally, but it cannot yet be argued postcranially. Further fossil discoveries will undoubtedly help resolve some of these issues, but findings to date imply a type of bipedalism in *H. habilis* more humanlike and more efficient than that of either *Au. afarensis* or *Au. africanus*.

Early *Homo* from Outside Africa

Outside of Africa a number of postcranial remains have been discovered at the 1.8 Ma site of Dmanisi in Georgia (Lordkipanidze et al. 2007). The species-level affinities of the Dmanisi hominins are the subject of some disagreement, but there is little debate that they belong to the genus *Homo*. Descriptions of the material suggest that the Dmanisi hominins had a combination of derived and primitive morphologies in their postcranial skeleton (Lordkipanidze et al. 2007; Pontzer et al. 2010). There is evidence for a longitudinal arch in the foot, a humanlike ankle and an elongated lower limb. However, there is also low humeral and tibial torsion compared to modern humans. In the original description of the material (Lordkipanidze et al. 2007), it was argued that the foot of the Dmanisi hominins would have struck the ground in a more medial orientation, which is often described as being "pigeon toed" in modern humans. However, a reanalysis of the published data has clearly refuted this suggestion and shows that the variables in question fall within the ranges of modern human variation (Wallace et al. 2008).

Early *Homo*: Summary

There is likely to have been some degree of locomotor diversity between different species of early *Homo*. The anatomy of the *Homo ergaster* postcranial skeleton (mainly based on KNM-WT 15000) is extremely humanlike and derived, and it would have been an obligate biped capable of long distance travel (Wang et al. 2004). In fact it has been suggested that this would have included endurance bipedal running, something that earlier hominins are unlikely to have been able to have done (Bramble and Lieberman 2004). On the other hand there is far less certainty concerning *Homo habilis*. Although there is evidence of a distinct shift between the morphology and associated locomotor function of its postcranial remains and those of *Australopithecus*, it would not have been as efficient a biped as *H. ergaster* and is likely to have had a unique pattern of gait. Therefore, while it is certain that by the beginning of the Pleistocene fully obligate bipedalism had developed in at least one lineage of *Homo*, it cannot be argued that this had occurred in *all* species within that genus. This would suggest that different early species of *Homo* were perhaps ecologically distinct from each other, with different locomotor behaviors and activity patterns.

Bipedalism in Later *Homo*

As mentioned above, nearly all later members of the genus *Homo* (e.g., *H. antecessor*, *H. heidelbergensis*, *H. neanderthalensis*) have postcranial skeletons entirely consistent with obligate bipedalism. Differences that do exist between these taxa and *H. sapiens* are small at best, though may have had some subtle effects on locomotor behavior. For instance, it has recently been shown that *H. neanderthalensis* had a slightly longer calcaneal tuber than modern humans, which would have increased its energy expenditure costs during running (Raichlen et al. 2011).

The one exception is the diminutive *H. floresiensis* from the Middle and Late Pleistocene of Flores, Indonesia. A number of metrical analyses of the postcranium show that the wrist retained several primitive, australopith-like features (Tocheri et al. 2007), the shoulder was more like that of *H. ergaster* than *H. sapiens*

(Larson et al. 2007), and the foot was markedly long compared to the leg and was unlikely to have had a longitudinal arch (Jungers et al. 2009). With such a combination of morphologies, while *H. floresiensis* was undoubtedly a biped, it was likely to have had a gait very different to that of modern humans.

Summary of Locomotor Behaviors Within the Hominin Clade

As we have seen, there are varying degrees of fossil evidence for the origins of bipedalism. More often than not, we are faced with the problem of being unable to place skeletal remains diagnostic of bipedality within a particular taxonomic hypodigm, and those fossil specimens which are associated with a particular species often show bewildering combinations of primitive, derived, and unique characteristics. However, on the basis of existing evidence, a number of broad conclusions can be made (Fig. 2). It is possible that the earliest hominins, such as *A. ramidus*,

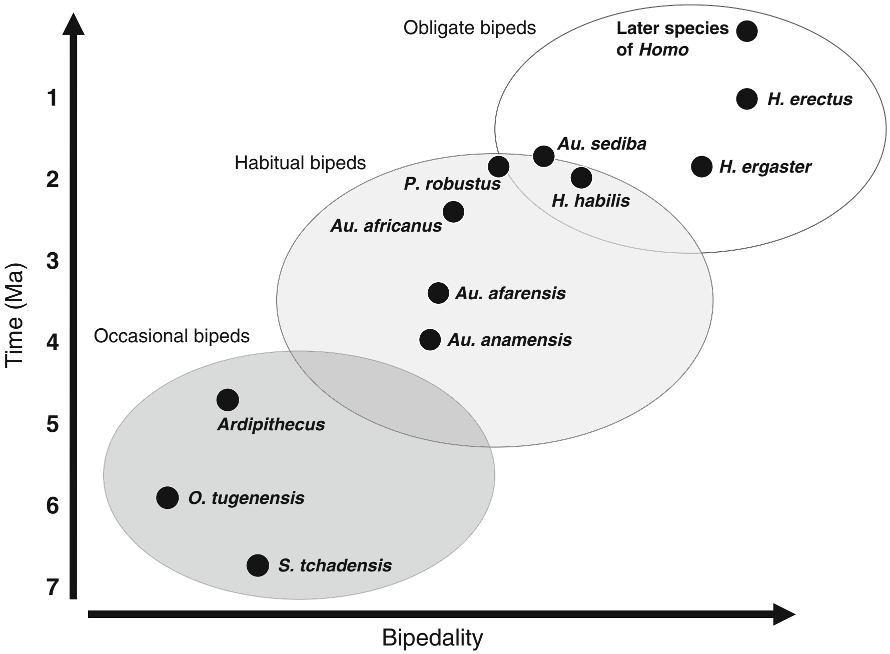

Fig. 2 The degree of bipedality in known fossil hominins relative to time. Only taxa with documented traits relating to bipedal locomotion are included. *Ardipithecus*, *O. tugenensis*, and *S. tchadensis* are classed as occasional bipeds on the basis of having very few or weak traits related to bipedality. *Australopithecus afarensis*, *africanus*, and *sediba* are classed as habitual bipeds on the basis of major anatomical remodeling of structures functionally related to bipedality, but retention of a number of apelike climbing specializations. *H. ergaster*, *H. erectus*, and later species of *Homo* are classed as obligate bipeds, but there is enough debate over *H. habilis* to place it between habitual and obligate bipedalism

O. tugenensis, and *S. tchadensis*, show important enough features to imply a slight shift to increased terrestrial bipedality. However, with the exception of *Ar. ramidus*, the evidence is extremely meagre, and further finds may show that any shift to bipedality could have been more or even less substantial. Following these taxa, there appears to have been at least two distinct shifts in the development of hominin locomotion. Firstly, between 4.5 and 3 Ma, a number of habitually bipedal hominin species emerged, as typified by the Laetoli footprints and the extensive postcranial remains from Hadar. Within this time frame it is possible that different species varied in the way that they became bipedal and that there were several different "types" of bipedalism being practiced (Harcourt-Smith and Aiello 2004; Haile-Selassie et al. 2012). The period between 2.5 and 1.8 million years heralds a second shift to fully obligate bipedalism. This period coincides with the emergence of the genus *Homo*, and by 1.8 Ma at least one member of this genus (*H. ergaster*) was a fully obligate biped with a modern human body plan. Other early species of early *Homo*, like *H. habilis*, may well have had a locomotor repertoire that was transitional between that of *Australopithecus* and *H. ergaster*. Subsequent to the advent of *H. ergaster* and *H. erectus*, all known hominins were fully obligate bipeds, although the enigmatic remains of the Middle-to-Late Pleistocene *Homo floresiensis* retain a number of primitive postcranial traits that would have made their gait, although bipedal, entirely distinct from that of *Homo sapiens* (Jungers et al. 2009).

Why Was Bipedalism Selected for?

As has been discussed, much contemporary debate over the origins of bipedalism rests on the locomotor affinities of particular taxa or individual specimens. This is understandable given that fossils provide concrete evidence. However, it is critical to also ponder why bipedalism was selected for and why it became such a successful form of locomotion for our species. Most early theories as to why humans became bipedal center on the "freeing of the hands" as the principal force of selection. This can be traced back to Darwin, who argued in the *Descent of Man* (1871) that bipedal locomotion must have evolved to allow for the construction and use of hunting weapons. Since that first explanation there has been as abundance of different theoretical explanations, ranging from the plausible to the wholly implausible. When considering these different potential selection pressures, it is important to consider that bipedal locomotion is a highly derived and unique form of primate locomotion. In that context, we have seen that the skeletal modifications associated with bipedality are considerable. It is therefore strong selection pressures that specifically required prolonged periods of upright walking that are likely to provide the key as to why bipedalism evolved (Lovejoy 1981; Rose 1991).

Prior to the discovery of the *Au. afarensis* remains from Hadar, the orthodox view remained that tools and tool use were intrinsically involved with the emergence of habitual bipedalism. Echoing Darwin (1871), some argued that tool use itself explained the selection for bipedalism (e.g., Washburn 1960), while others suggested that behavior was a more likely explanation (e.g., Bartholomew and Birdsell 1953; Washburn 1967). Both these theories are now contradicted by the temporal sequence of events provided by the contemporary fossil and archaeological records (Rose 1991). Evidence of bipedal locomotion currently predates the earliest stone tools by at least 1.5 Myr and probably more, which precludes the involvement of any stone-tool-associated behavior in the origins of bipedality. More recent hypotheses have tended to be strongly linked to paleoenvironmental changes from the end of the Miocene through to the beginning of the Pleistocene. In this respect the traditional view has been that the emergence of bipedalism most likely correlated with generally cooler and dryer global conditions and an associated increase in more open grassland habitats (Van Couvering 2000), often referred to as the "savanna hypothesis." Predominantly forested environments were gradually replaced by more mosaic environments made up of different proportions of open grassland, bushland, and open woodland (Reed 1997). To cope with these environmental changes, it was argued that hominins had to adapt a series of new behavioral strategies. Change in habitat composition would have resulted in a shift in food availability and thus necessitated a shift in food acquisition behaviors (e.g., Rose 1991; Foley and Elton 1998). Hominins would either have to have ranged further to find food or develop strategies to procure new and different types of food. In this scenario, it was therefore very likely that hominins would have had to have engaged in more terrestrial travel over more open habitats, resulting in the emergence of bipedality as an important part of the locomotor repertoire.

However, the discovery of late Miocene hominins (see section "Earliest Hominin Evidence") and the increasing complexity associated with accurately reconstructing hominin paleoenvironments (Behrensmeyer and Reed 2013) has complicated the savanna hypothesis to some degree. The paleoenvironments of the earliest hominins through to late *Australopithecus* have been varyingly reconstructed from very open and dry to relatively closed and forested (Behrensmeyer and Reed 2013). Coupled with recent suggestions that hominin bipedalism originated in arboreal environments (e.g., O'Higgins and Elton 2007; Thorpe et al. 2007; Almécija et al. 2013), it is possible that the classic savanna hypotheses is in need of reevaluation when considering the shift from occasional to habitual bipedalism in early hominins. For the shift from habitual to obligate bipedalism in the early Pleistocene, the hypothesis is on stronger ground, as this period coincides with an unambiguous opening up of hominin habitats (Reed 1997; Van Couvering 2000).

Despite these complexities, a number of theories strongly associated with the savanna hypothesis warrant discussion. Lovejoy (1981) argues that food-carrying and procurement by males was the driving selection pressure. This would tie in with some interpretations of the fossil material from Hadar that suggests that there was a degree of locomotor sexual dimorphism in *Au. afarensis* (Stern and Susman 1983). Recent experimental work also supports Lovejoy's (1980) theory in showing that introducing widely distributed "food piles" leads to an increase in chimpanzee and bonobo locomotor bipedality, mainly associated with food-carrying (Videan and McGrew 2002). Such a situation could be analogous to the more spread-out concentrations of food sources available to hominins in a more open grassland environment. Increased bipedalism in such a setting would greatly increase the ability to carry food to desired locations. Other theories argue for terrestrial food-gathering (Jolly 1970; Wrangham 1980) or even hunting (Carrier 1984; Shipman 1986; Sinclair et al. 1986). Jolly's (1970) model uses the open-savanna gelada baboon as a modern-day analogue to suggest that early hominin bipedalism was linked to rapid seed-collecting behavior. Hunt (1990, 1994, 1996) has argued that chimpanzee postural behaviors may provide the key to our understanding of this issue. Over 80 % of chimpanzee bipedalism is related to postural feeding. Using this as a behavioral analogue, Hunt argues that early hominin postcranial adaptations in *Australopithecus* were related to similar postural feeding behaviors, and that true bipedal locomotion emerged with the advent of *Homo* (see Wood 1993). It is certainly possible that bipedal postural behavior may have preceded bipedal locomotion, but posture alone is likely to be too weak a selection pressure to have resulted in the significant anatomical remodeling seen in the *Au. afarensis* and *Au. africanus* pelvis and lower limb structures (Lovejoy 1981; Rose 1991). It has also been suggested that bipedal threat displays may have been an important selective precursor to bipedal locomotion (Jablonski and Chaplin 1993).

One of the most interesting and widely accepted explanations of why hominins became bipedal is the thermoregulatory hypothesis suggested by Wheeler (1984, 1988, 1991, 1993, 1994). This argument rests on strong physiological explanations related to the reduction of thermal stress and directly relates to the more open habitats that hominins would have become exposed to through the Pliocene. On the open savanna, quadrupedal animals expose considerably more of their body's surface area to the sun. By standing fully upright, Wheeler calculated that a hominin would absorb 60 % less heat at midday. Furthermore, being upright exposes the subject to any potential breeze, which would have a further cooling effect. These factors would greatly reduce the rate at which hominins would have overheated on open ground, meaning that they could have ranged further without having to have increased water intake. In a more open environment, where food sources were likely to have been more spread out, such an advantage would have greatly enhanced the ability of hominins to successfully collect food (Chaplin et al. 1994). One other physiological explanation for the development of bipedalism warrants comment. Rodman and McHenry (1980) have argued that there is a considerable energetic advantage to become bipedal. However, it has been shown that *Pan* and *Gorilla* locomotion is not any less efficient physiologically than that of modern humans (Steudel 1994).

Perhaps the most interesting point relating to all the above theories is that made by Robinson (1972), who states that there is unlikely to have been *one* specific reason why bipedalism was selected for. It was more likely a combination of several selective factors strongly relating to feeding strategies and reproductive behavior that provided the impetus for this shift in the hominin locomotor repertoire. Furthermore, bipedalism would have provided not only the ability to range further for food and other resources; it would have exposed hominins to novel parts of the surrounding landscape, different types of predators, and new food sources. This in turn would have led to new hominin behavioral strategies to cope with such changes. It has also been argued that, on the basis of increasingly variable environmental conditions during the Late Miocene and Pliocene, associated behavioral versatility would have been a critical selective factor for early hominins (Potts 1998). If so, there is little doubt that selection for bipedality would have considerably facilitated such behavioral versatility.

Conclusion

There is no doubt that the evolution of bipedalism is a critical issue in the study of human origins. However, as we have seen, there has often been a considerable degree of rather polarized debate and disagreement as to how, when, why, and in whom hominin bipedalism evolved. In particular, the emergence of so many important fossil finds in the last 40 years has resulted in the literature becoming increasingly "fossil driven" in its concentration on *how* bipedal a particular hominin taxon might have been. This has often clouded our understanding of the larger issues at stake surrounding the emergence of this unique form of primate locomotion. As Rose (1991) has pointed out, selection for bipedality was not an event, but rather a series of processes. In that context, what can be said about these processes? It is certain that the selection pressures for bipedality must have been strongly linked to reproductive success, and it is therefore likely that such pressures would have been related to the efficient gathering and transport of food and other resources across increasingly varied habitats. As discussed earlier in this chapter, the current fossil record points to at least one minor and two major steps in the emergence of obligate, humanlike bipedality. The earliest hominins were little more than occasional bipeds, while the australopiths can certainly be considered as habitual bipeds who still engaged in some arboreal locomotor behaviors. By the emergence of early *Homo*, certain species within that genus were unequivocally obligate bipeds much in the way that we are today. It is perhaps seductive to view such steps as punctuated events, and that may have been the case. But it is also possible that the fragmentary fossil record merely creates the illusion of such steps. Only the recovery and analysis of further fossil remains relating to bipedality, particularly from the Late Miocene hominoid record, will further our understanding of this complex and unique process.

Cross-References

- ▶ Defining the Genus *Homo*
- ▶ Fossil Record of Miocene Hominoids
- ▶ General Principles of Evolutionary Morphology
- ▶ *Homo floresiensis*
- ▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins

▶ Postcranial and Locomotor Adaptations of Hominoids
▶ Role of Environmental Stimuli in Hominid Origins
▶ The Biotic Environments of the Late Miocene Hominoids
▶ The Miocene Hominoids and the Earliest Putative Hominids
▶ The Species and Diversity of Australopiths

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The Evolution of the Hominid Brain

Ralph L. Holloway

Contents

Abstract

The evolution of the human brain has been a combination of reorganization of brain components and increases of brain size through both hyperplasia and hypertrophy during development, underlain by neurogenomic changes that have involved epigenetic changes largely effecting regulation of growth dynamics. While both genomics and comparative neuroanatomical studies are invaluable to understanding how brains and behavior correlate, it is paleoneurology, based on endocast studies (chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1), which are the direct evidence demonstrating volume changes through time. Some convolutional details of the underlying cerebral cortex do appear on

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R.L. Holloway (✉)
Department of Anthropology, Columbia University, New York, NY, USA
e-mail: rlh2@columbia.edu

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the endocranial surface. These details allow one to recognize reorganizational changes that include (1) a reduction of primary visual cortex and relative enlargement of posterior association cortex, (2) expanded Broca's regions, and (3) cerebral asymmetries. The size of the hominid brain increased from about 450 ml 3.5 Ma ago to our current average volume of 1,350 ml, with a slight reduction since Neolithic times. Many more data from additional fossils will be necessary to decide how and when these two changes through time occurred and whether these were gradual or punctuated.

Introduction

The evolution of the human brain has largely been a matter of integrating both increases in the size of the brain and the brain's organization through the past 3–4 myr mainly based on species of the genus *Australopithecus* and two of its species, *A. afarensis* and *A. africanus*.[1] Earlier possible hominin forms such as *Sahelanthropus* or *Ardipithecus* in the time range of 3–6 myr do not have sufficient endocranial remains to do more than estimate volumes. Three lines of evidence are used by paleoneurologists to ascertain how these events might have occurred: (a) direct evidence from the brain endocasts of fossil hominids (paleoneurology) and (b) the indirect evidence from comparative neuroscience, where variations in brain structures can be related to variations in behavior and be compared between species. This latter evidence is "indirect" because extant living animals are not ancestral to humans and have undergone their own evolutionary changes. Indeed, the last common ancestor for apes and the hominid line existed some 5–7 Ma ago. (c) Newer neurogenomics evidence also promises to provide important clues to how and when certain aspects of brain changes occurred during human evolution (e.g., Preuss 2012; Zeng et al. 2012).

Our best paleoneurological evidence suggests that the human brain evolved from an early hominid 3–4MY, *A. afarensis*, having a size of roughly 400 ml to our present average of 1,330 ml. These brain size increases, at different taxonomic levels, were mostly allometric, i.e., related to body size, but not always. Integrated with these changes in brain size was reorganization of the cerebral cortex, as well as changes in subcortical structures such as the hippocampus, amygdala, etc., to mention a few important structures that relate to aspects of social behavior but that cannot be seen on endocasts. Reorganization simply refers to both qualitative and quantitative changes through time of neural structures. Endocasts, of course, cannot provide information regarding neural variables such as subcortical volumes, cell densities, dendritic branching and connectivity, or any neurochemical or neurophysiological information. Thus from the point of view of knowing what

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[1] This paper is adapted and expanded from an earlier chapter written for the Encyclopedia of Human Biology, 3rd Ed. Elsevier, In press.

exactly the data indicate regarding human brain evolution, the direct evidence of endocasts is critically important, however poor the data they contain actually may be.

At least three areas of the reorganization of the cerebral cortex were affected at different times: (a) a relative reduction of primary visual striate cortex (V1, PVC) and an attending relative increase in posterior parietal association cortex; (b) a change in Broca's region, resulting in a more humanlike pattern; and (c) increasing degrees of cortical asymmetry, as well as increases in overall brain size and number of neurons.

How exactly did the human brain evolve, and when did changes in it happen? Obviously, to answer this question fully would require a time machine and thousands of generations of observations to ascertain both the variability and direction of selection pressures in the past. We can, however, flesh out an initial understanding of how we got to be the animal *par excellence* that utilizes its brain for intelligent rationalizations, based largely on the use of arbitrary symbol systems and on behavioral adaptations involving a complementary social existence between males and females permitting prolonged infant growth and nurturance (chapters "▶ Great Ape Social Systems" and "▶ Theory of Mind: A Primatological Perspective," Vol. 2). The evidence consists of two components: (a) the "direct" evidence from the fossil record and (b) the "indirect" evidence of the comparative neuroscientific record of extant living animals, particularly those most closely related to us such as the chimpanzee and bonobo. There is also a third possibility: since the Human Genome Project has sequenced almost all of the genetic code, the future study of evolutionary neurogenomics might provide more data about the actual genetic history of our genus through time, as well as that of the great apes mentioned above (see, e.g., Hernando-Herraez et al. 2013; Gokcumen et al. 2013). As this latter possibility is little more than a gleam in our eye at present, this article will concentrate on the evidence provided by the first two components.

Lines of Evidence

Direct Evidence

The term *paleoneurology* is used to describe evidence relating to the size and morphology of the casts made from the inside of actual fossil cranial remains. Occasionally, the casts are "natural," i.e., where fine sediments have filled the inside of the cranial cavity, becoming infiltrated and compacted through time. These casts sometimes retain some of the morphological details that were imprinted on the internal table of bone of the cranium when the animal was alive. The famous australopith (*A. africanus*) Taung child's skull, described by Dart (1925), is one of the best-known examples, as are Sts 60 and SK 1585, the latter a fine example of *Australopithecus robustus*. Curiously, these "natural" endocasts are only found in the South African australopiths (chapter "▶ Analyzing Hominin Phylogeny: Cladistic Approach," Vol. 3) and date from about 3.0 myr to about 1.5 myr (see Fig. 1). Traditionally, paleoneurologists have made casts of the insides of fossil

Fig. 1 Casts of the Taung (*left*), Sts 60 (*right*), and SK 1585 (*bottom*) "natural" endocasts of Australopithecines

skulls using rubber latex, or silicone rubber, extracting these from the cranial remains. The partial cast is then sometimes reconstructed by adding plasticine (modeling clay) to the missing regions. The whole is then measured by immersion into water, and the amount of water displaced is regarded as the volume of the once-living brain. Other measurements (linear chords and arcs) and observations (convolutions and asymmetries) may be made on the original cast. More recently, "virtual" endocasts have been made from CT scans of intact or partial crania, an approach that has the advantage of being noninvasive (chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1). As it is computer driven, there are various algorithms for deriving the size of the endocast and other metrics (chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1; Weber et al. 2012; see also Zollikofer and Ponce de León 2013). Of course, CT scans (medical and micro) are not continuous, as is the case with actual casting materials such as silicone-based materials that flow into all the cracks, crevices, and convolutional details available.

During life, the brain is surrounded by three dural tissues (the dura mater, the arachnoid tissue and its cerebrospinal fluid, and the pia mater) that interface between the actual brain tissue (cerebral cortex, mostly) and the internal table of bone of the skull. The gyri and sulci (convolutions) of the once-pulsating cerebral cortex are thus imperfectly imprinted on the interior of the skull, and the degree of replication often varies in different regions, e.g., sometimes the frontal lobe imprints more details than the parietal lobe, as well as by age. The degree of replication also varies in different animals. Two extremely important considerations emerge from this: (a) the resulting imprints are never complete and are thus

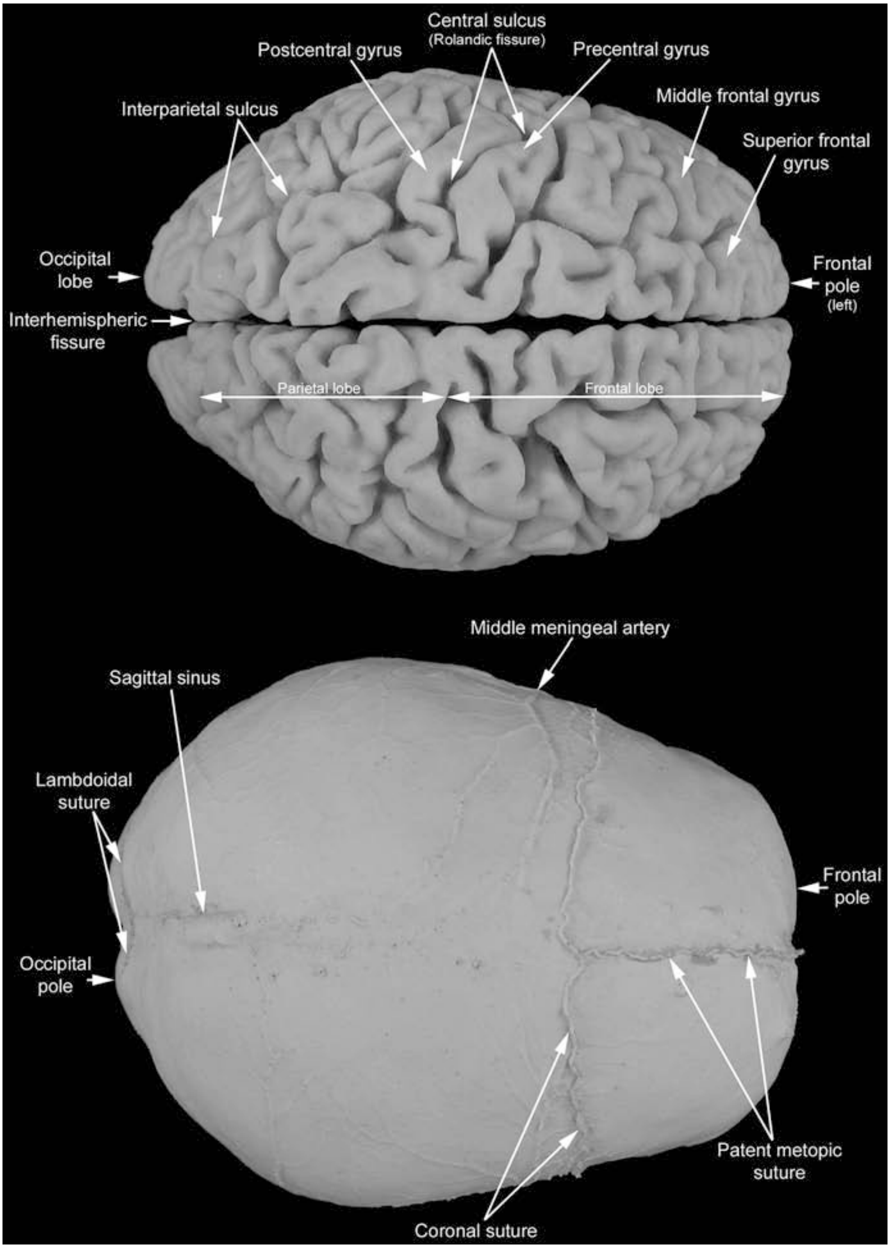

Fig. 2 (continued)

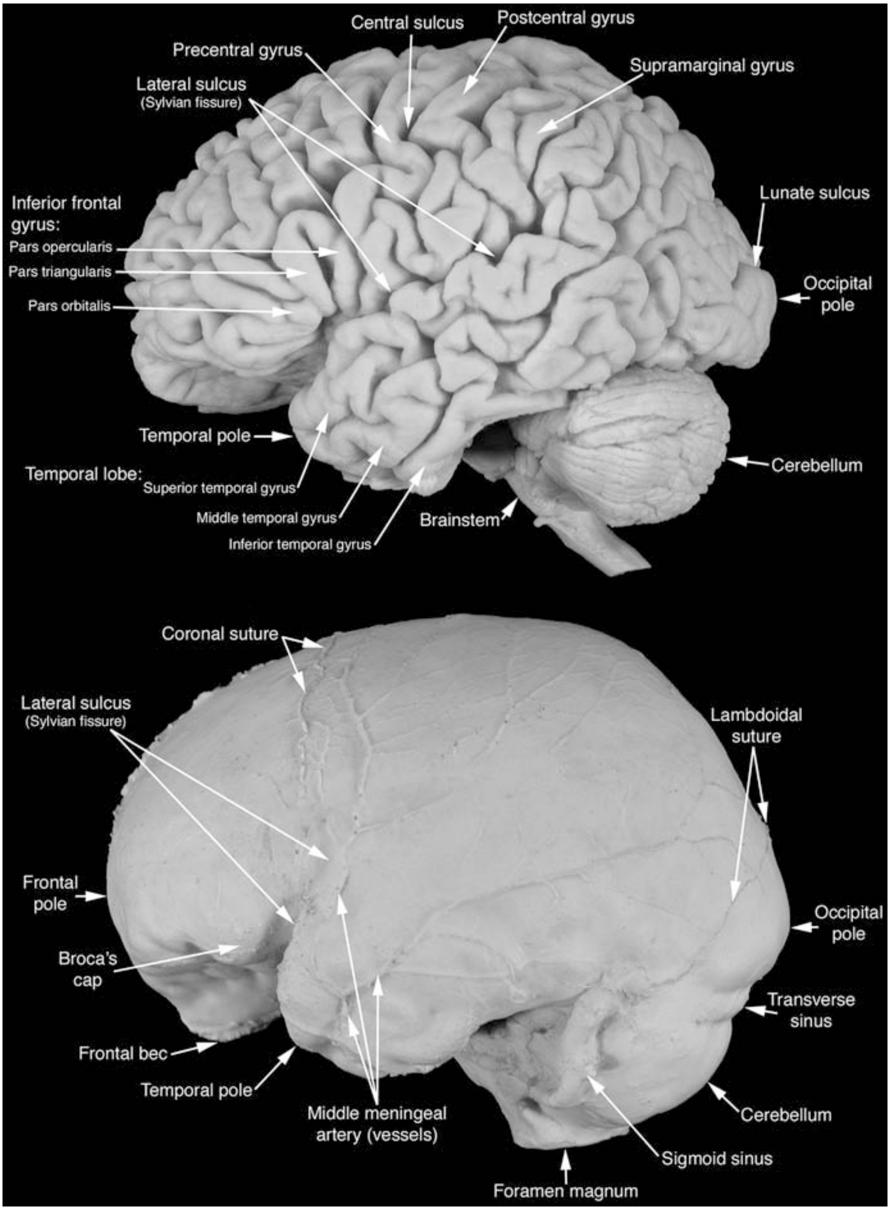

Fig. 2 Dorsal (see *previous page*) and lateral (see *above*) views of a modern human brain and the endocast to demonstrate the loss of detail on the endocast surface

in that sense "data poor," never including subcortical structures, and (b) the controversial interpretations of what the underlying brain once looked like are guaranteed (see Fig. 2). Nevertheless, endocranial casts do provide extremely important information regarding (1) overall size, (2) shape, (3) rough estimates of

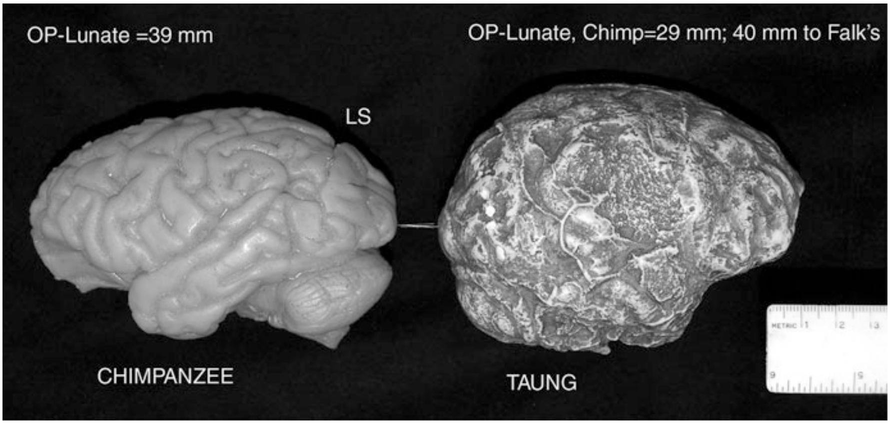

Fig. 3 Lateral view of a chimpanzee brain and the Taung *A. africanus* endocast. The lunate sulcus separates PVC from association cortex and is in an anterior position in apes. The *white dots* on the Taung endocast show where the average chimpanzee lunate sulcus would fall and that location violates the sulcal morphology on Taung. Placing it more anteriorly would be a monkey-like configuration. The Taung lunate sulcus would most probably be posterior, in a humanlike position, which is near the lambdoid suture

the lobal dimensions of the brain, and (4) cortical asymmetries that have relationships to hemispheric specializations and behavioral processes including handedness. In addition (5), if the imprints of the underlying gyri and sulci are available, they can provide important information regarding the organization of the cerebral cortex and whether the patterns of these are the same or different as in known extant primate brains. The infamous "lunate sulcus" is a good example, as it is a demarcation boundary between purely sensory primary visual striate cortex (PVC) and multimodal association cortex in both Old World monkeys and anthropoid apes. When the lunate sulcus appears in an anterior position, it is most similar to the condition known in modern apes. When it is found in a posterior position, it is in a more humanlike condition. Ascertaining its correct position is thus essential in deciding whether or not such a fossil hominid had a brain organized along human or ape lines. In modern humans, the "lunate" is only partially homologous with that found in apes and is usually fragmented (Allen et al. 2006). Hominins such as *Homo erectus*, *H. heidelbergensis*, *H. georgicus*, and *H. neanderthalensis* unfortunately do not have occipital lobes that allow clear-cut identification of the lunate sulcus if it were a singular unfragmented sulcus. Figure 3 shows a comparison between a chimpanzee brain with a lunate sulcus and that of the Taung child, *A. africanus* (See also Holloway 1984, 2000). Finally (6), meningeal arteries and veins that nourished the dura mater also imprint on the internal table of bone and sometimes show patterns that are useful for deciding taxonomic issues; these have no known relationship to behavioral functions of the brain. (See also Grimaud-Hervé in Holloway et al. 2004, for further discussion and illustrations.) Figure 4 shows that a more recent *A. africanus* specimen from Sterkfontein, S. Africa, Stw 505, shows a clear lunate

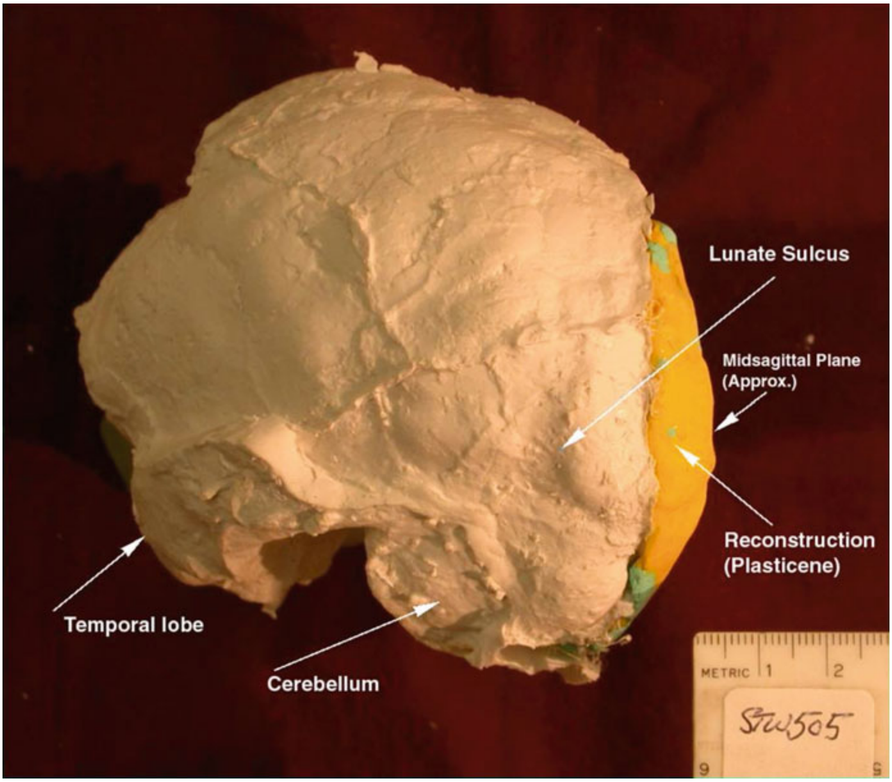

Fig. 4 Oblique view of the Stw 505 *A. africanus* specimen, showing a prominent lunate sulcus in a posterior position. This specimen makes it clear that at least some australopithecines had reduced primary visual cortices and expanded posterior parietal lobes, evidence showing that reorganization probably preceded brain size increases

sulcus in a relatively posterior position compared to chimpanzee brains. Falk (2014) has made the bizarre suggestion that is perfectly crescentic lunate sulcus is the lateral calcarine sulcus, which is not possible given the medially directed curvature of both inferior and superior ends of the depicted lunate sulcus in Stw505. When in the course of subsequent hominin evolution, the lunate sulcus changed into a more fragmented partially homologous structure as found in modern humans is unknown, as neither *Homo erectus* nor Neanderthals show detailed gyri in the occipital region (chapters "▶ Later Middle Pleistocene *Homo*" and "▶ Neanderthals and Their Contemporaries," Vol. 3).

The frontal lobe is of course a major focus of examining endocasts in the hope of understanding the evolutionary trajectories through time of the most crucial part of neuroanatomy underlining our very humanness, intelligence, and social behavior. Here, we are plagued with by the fact that very few sulcal details are available on the endocasts of early hominins, particularly the australopiths. A recent paper by Carlson et al. (2011) describes the frontal portion of an endocast of MH1 (Malapa

Hominin 1) that they have named *Australopithecus sediba* and that shows some possibility of prefrontal organization toward a more human condition.

Indirect Evidence

This line of evidence is “data rich,” providing comparative neurological information on living species, such as brain size (both absolute and relative, i.e., related to body size), the actual makeup of the brain from the gross to microscopic levels, including neural nuclei, fiber systems and interconnections, and distribution of neurotransmitters and neuroreceptors. Additionally, the brain can be studied ontogenetically, and neuroscientists can actually study the relationships between how the brain varies neurologically and how these variations relate to the behavioral variation. Modern examinations including CT, MRI, fMRI, and tensor diffusion techniques can be applied, yielding different kinds of data relevant to different aspects of growth and development, genetic and epigenetic unfolding, and behavioral consequences (chapter “▶ Virtual Anthropology and Biomechanics,” Vol. 1). Neurogenomic information will also add considerable details as to how living brains vary and operate, both within and between different species, and hopefully inform us about selection events in the evolutionary past. This richness is simply lost to the paleoneurologist. However, it is necessary to realize that the extant living species often used as comparisons to humans, e.g., bonobo, chimpanzee, and macaque (chapters “▶ Estimation of Basic Life History Data of Fossil Hominoids,” Vol. 1, “▶ Evolution of the Primate Brain,” and “▶ The Hunting Behavior and Carnivory of Wild Chimpanzees,” Vol. 2), are end points of their own evolutionary lines of development and are not our ancestors, however closely related to us they may be. It is thus the blending and complementation of these two approaches which provide the best set of evidence for when and how our brains evolved. Another aspect of the comparative evidence is the question of how well we can explain species-specific behavior on the basis of what we know from comparative neurology. Considering the behavioral differences between chimpanzees and bonobos and gorillas and orangutans, there are no current explanations to explain these in terms of neuroanatomical detail.

Characteristics of the Human Brain

Brain Size, Absolute and Relative

The human animal is obsessed with size, and those who study the brain comparatively are perhaps more so than average. With a mean brain weight of 1,330 g and a body weight of 65,000 g (Tobias 1971), the human species has the largest absolute brain size within the primate order, but is actually dwarfed by elephants and some of the whales, in which brain weight can exceed 7,500 g. Of course, body weights are also very much higher in elephants and whales. But even for its body weight,

Table 1 Fossil hominid brain volumes

Group	Average Number	Location	Brain volume	Range	Dating (myr)
A. afarensis	3	E. Africa	435	385–500+	3–4
A. africanus	8	S. Africa	440	420–500+	2–3
A. aethiopicus	1	E. Africa	410	na	2.5
A. garhi	1	E. Africa	Ca. 450	na	2.5
A. sediba	1	S. Africa	Ca. 420	na	2–3
A. robustus	6	E. and S. Africa	512	500–530	1.6–2.0
H. rudolfensis	2	E. Africa	775	752–800	1.8
H. habilis	6	E. Africa	612	510–687	1.7–2.0
H. georgicus	3	Georgia and Europe	677	600–775	1.7
H. ergaster	2	E. Africa	826	804–848	1.6
H. erectus	2	E. Africa	980	900–1,067	1.0–1.6
H. erectus	8	Indonesia	925	780–1,059	1.0
H. erectus	8	China	1,029	850–1,225	0.6
Archaic *H. sapiens*	6	Indonesia (Solo)	1,148	1,013–1,250	0.13
Archaic *H. sapiens*	6	Africa	1,190	880–1,367	0.125
Archaic *H. sapiens*	7	Europe	1,315	1,200–1,450	0.5–0.25
H. sapiens (Neand.)	25	Europe and M. East	1,415	1,125–1,740	0.09–0.03
H. sapiens sapiens	11	World	1,506	1,250–1,600	0.025–0.01

Source: Holloway 1997

Homo sapiens does not have the largest relative brain weight (about 2 % of body weight), being outdone by several monkeys, some rodents, and even some fish. Normal modern human brain size varies between roughly 900 and 2,000 g, although a very small number of exceptions do occur, with sizes in the 750–900 and 2,000–2,200 g range. Human populations vary, as do the sexes. In general, Arctic peoples tend to have larger brains than those living in the tropics, and the smallest brains appear to be found among Ituri forest pygmies who also display small stature. Males in all populations for which good autopsy or cranial data have been gathered show brain sizes on the average of 100–150 g greater than females, an amount roughly the same as the range of modern human racial variation. It should be pointed out that these differences, and their possible relationship to cognitive skills, are highly controversial, and simple correlations are deceptive (Holloway 1996, 2008; Nyborg 2003). Table 1 provides a listing of the major fossil hominid taxa and their respective brain sizes (See Neubauer et al. 2012 for confirmation of my australopithecine volumes). Notice that the range of values

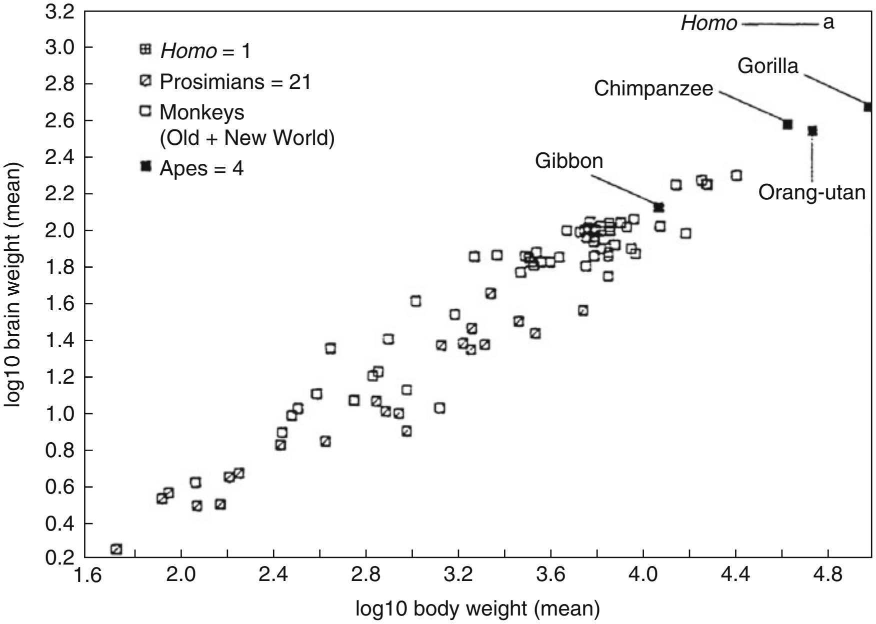

Fig. 5 Graph showing human deviation from a plot of log brain weight against log body weight for primates, with *Homo* at the extreme upper right position

from the earliest australopithecine to modern *Homo* is roughly 1,000 ml or about the same amount as the normal range of variation within our species.

Encephalization (Encephalization Coefficient, EQ)

Nevertheless, the human animal does come out on top of the evolutionary heap when its absolute brain and body weights are considered together. When the log (base 10) of brain weight is plotted against the log10 of body weight for a group of relevant taxa, the result is usually a linear relationship, where (log10) brain weight = a + b (log10) body weight. For a large array of primate data (e.g., Stephan et al. 1981), the slope of the line (b in the equation above) is about 0.76, and the correlation coefficient is 0.98, indicating that the relationship is almost perfect (chapter "▶ Estimation of Basic Life History Data of Fossil Hominoids," Vol. 1). This relationship will naturally vary depending on the databases and the transformations used. This is known as an allometric equation, and these are used frequently in biology to assess the underlying relationships between the size of parts of the body and the whole (see Fig. 5). The slope sometimes has an interpretation suggesting functional relationships between the brain and other variables. For example, in the above example, the slope is 0.76, extremely close to 0.75 or 3/4, which often describes a metabolic relationship (Martin 1983). The slope of 0.66, or

Table 2 Some examples of encephalization quotients

Species	Brain wt. (g)	Body wt. (g)	EQ *Homo*[a]	EQ Jerison[b]	EQ Primates[c]	EQ Stephan[d]
Lemur	23.3	1,400	21	1.56 (22.6)	0.94 (32.7)	5.66 (19.6)
Baboon	201	25,000	28	1.97 (28.5)	0.90 (31.3)	7.94 (27.5)
Gorilla	465	165,000	23	1.56 (22.5)	0.61 (21.2)	6.67 (23.2)
Orang	370	55,000	31	2.15 (31.1)	0.91 (31.7)	8.90 (30.9)
Chimp	420	46,000	39	2.63 (28.1)	1.81 (41.1)	11.3 (39.3)
Human	1,330	65,000	100	6.91 (100)	2.87 (100)	28.8 (100)

Source: Holloway 1997. Note: each formula is based on a different set of data. The EQ *Homo* equation simply uses the average brain and body weight for *Homo sapiens* and assumes an intercept where both brain and body weights are zero. The value of whichever animal is calculated is then given as a direct % of modern *Homo sapiens*. EQ Jerison is based on data for almost 200 mammals, while the EQ Primates is based on Martin's (1983) data set for primates only. The EQ Stephan equation is based on insectivores only. The numbers in the parentheses are the % of the *Homo sapiens* value

[a] Formulae: EQ *Homo* = Brain wt/1.0 Body $\text{wt}^{0.64906}$

[b] EQ Jerison = Brain wt/0.12 Body $\text{wt}^{0.66}$

[c] EQ Primates = Brain wt/0.0991 Body $\text{wt}^{0.76237}$

[d] EQ Stephan = Brain wt/0.0429 Body $\text{wt}^{0.63}$

2/3, has been championed by some (e.g., Jerison 1973) as indicating an important geometric relationship between volume and surface area. It is important to realize that these slopes vary depending on the taxa examined. In general, as the taxa become more similar, the slope decreases. Species within a genus generally have a slope around 0.3; within a species, the slope is smaller yet, being about 0.2, and the correlation coefficient is also reduced (see also Martin and Isler 2010).

Just as the human animal is curious, it is also vainglorious, always trying to find a measure that places it at the top. Thus we can fabricate a device, the *Encephalization Coefficient* or EQ, which shows that relative to any database, the human animal is the most encephalized animal living. The point for *Homo sapiens* shows a clear positive residual above the expected regression line, and in fact the human value is about three times that expected for a primate with its body weight. Table 2 provides a number of different equations based on differing databases, which happily give *H. sapiens* the highest value. (Actually, young immature dolphins will provide a higher number, but when compared to an immature human, the value is higher in the latter.) Two additional points should be made: (a) EQs are relative to the databases used, and thus there is an inherent "relativity" to relative brain sizes; and (b) EQs do not evolve, only brain weight/body weight relationships do, and EQs are simply a heuristic device enabling comparisons between taxa; they have no reality outside of the database chosen, or species within a taxa, and are not designed to discuss within-species variation. For example, female humans are "more" encephalized than males, given their smaller body sizes, more body fat which is not innervated, and smaller brains, but the relationship might be simply a statistical artifact with no known gross behavioral manifestation given the sexes equal overall intelligence. It is more likely that small differences in neural reorganization might be related to behavioral differences such as language ability or math and spatio-visual manipulation rather than brain size or EQ.

I will discuss later how the processes of hypertrophy and hyperplasia have been positively selected for in the course of the last 2–3 myr of hominid evolution. (Hypertrophy refers to increases in size of the neural components, e.g., neurons, dendritic branching, nuclei, and fiber tracts; hyperplasia refers to increased production of cells through mitotic division.) It is most probably the case that these processes are controlled by regulatory genes, and one of the major differences between ourselves and our closest nonhuman primate relative, the chimpanzee (brain size = ca. 385 g), relates to the schedules by which hyperplasia and hypertrophy are turned on and off during ontogenetic development (Holloway 1980, 1995; Miller et al. 2012).

Brain Organization and Reorganization

It is well known that the brains of most animals are extremely similar to each other in terms of their overall organization, by which are meant neural nuclei and fiber systems. The human animal does not appear to show any different structures when compared to Old World monkeys such as the macaque or the great apes, including bonobo, chimpanzee, gorilla, and orangutan. Even the neural fiber tracts that are involved in human language appear in these primates (Deacon 1997). One might ask, then, given the obvious species-specific repertoires that exist in all animals, how can these behaviors differ without differences in the underlying nervous systems? This is one of the major challenges of studying brain evolution and in particular understanding what neural organizations account for the specificity of, say, human behavior, the ability to use language composed of arbitrary symbols. In other words, all mammals have a cerebral cortex, a thalamus, cerebellum, hypothalamus, etc., and basically these structures possess almost identical divisions of nuclei and do the same neural tasks. Clearly, brain size alone will never explain species-specific behavior, and the relationships between neural nuclei and fiber tracts will only go so far in explaining behavioral differences.

Allometric equations showing the relationship between individual bodily components and the whole are instructive here. If we were to plot the logs (base 10) of primary visual cortex (PVC) against brain volume, we would find that the human PVC is 121 *% less* than predicted, and similarly, the lateral geniculate nucleus of the thalamus is about 144 *% less* than expected for a primate of our brain size (see Fig. 6). In contrast, if one plots the amount of cerebral cortex against brain weight the result is a straight line, and the human point lies almost exactly on the line. In short, the human cerebral cortex is as large as would be expected for a primate of its brain size. But do portions of the cerebral cortex vary in size between different primates? In humans, the residuals mentioned above suggest that compared to chimpanzees, the amount of PVC is significantly smaller in humans, or alternatively put, the posterior association cortex of the parietal and temporal lobes is relatively larger in humans. Since there are no essential differences between

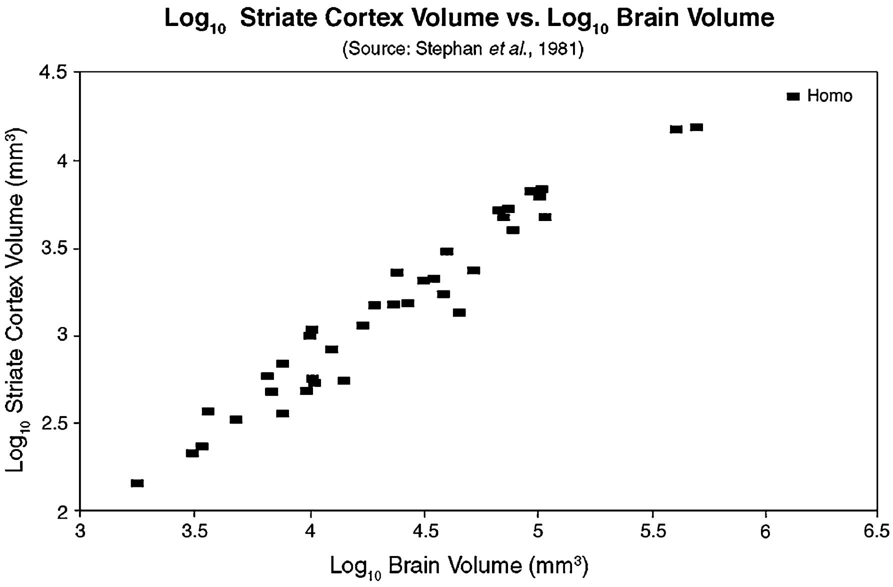

Fig. 6 Graph showing log striate cortex (area 17) versus log brain volume, where the value for *Homo sapiens* (*upper right*) is 121% less than expected from the log-log regression (see also Table 3, which shows other departures between actual and predicted values for different brain structures)

Table 3 Human brain structure residuals[a]

Dependent variable	Independent variable	Number species	Correl. coeff. (R)	Actual value (A)	Expected value (E)	(A)/ (E) ratio	%Diff. (A)/ (E) homo
Striate cortex	Brain weight (C)	37	0.971	22,866	50,598	0.45	−121.30
		19	0.977		38,097	0.60	−66.60
Lateral geniculate	Brain weight (C)	37	0.978	416	1,026	0.41	−146.60
		19	0.982		857	0.49	−106.00
Cerebellum	Brain weight (C)	44	0.990	137,421	128,932	1.07	6.20
		26	0.994		150,535	0.91	−9.50
Dienceph.	Brain weight (C)	44	0.995	33,319	51,512	0.65	−54.60
		26	0.998		47,899	0.70	−43.70
Septum	Brain weight (C)	44	0.983	2,610	2,085	1.25	20.10
		26	0.991		2,201	1.19	15.70
Amygdala	Brain weight (C)	16	0.990	3,015	4,633	0.65	−53.70
		7	0.985		3,753	0.80	−24.50
Lateral geniculate	Thalamus	21	0.979	416	731	0.57	−75.72
		10	0.988	416	636	0.65	−52.88

[a] Based on Stephan et al. (1981) data

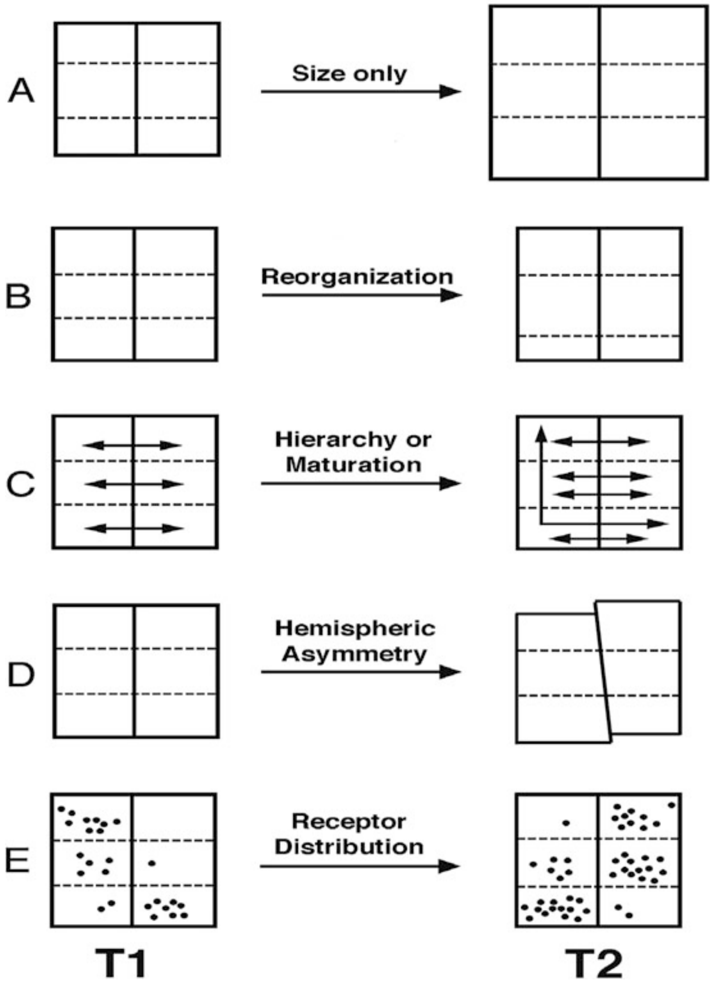

Fig. 7 Types of reorganization without necessary brain size increase. The *dashed lines* represent boundaries between frontal, parietal, and occipital lobes, which if changed in relative positions from T1 to T2 would suggest reorganization

chimpanzees and humans in their visual abilities and competencies, these differences most probably reflect selection for expanded functioning of the association cortex in humans. This is precisely what is meant by "reorganization" (Table 3).

When used in a comparative or evolutionary context, reorganization means changes in the sizes and proportions thereof of neural nuclei and their fiber tracts (see Fig. 7). Given that chimpanzees and hominids had a last common ancestor some 5–7 myr and that chimpanzees appear to have large PVC cortices, we infer that one aspect of human brain evolution has been some reorganization of the cerebral cortex, namely, an increase in posterior association cortex (or, equally, a reduction in PVC) involved in polymodal cognitive tasks, where visual, auditory, and motor information are brought together in a synthetic whole. The trick, of course, is to demonstrate objectively when, where, and why these changes took place. This example of PVC has been purposefully chosen because one of the sulcal landmarks of the cortex that defines the anterior border of PVC is the “lunate” sulcus, named for its crescentic shape, and there is some hope of identifying its position on some of the early hominid brain endocasts. In this regard, endocasts are most often frustratingly mute on other convolutional details.

Neuroanatomists have been trying for many decades to demonstrate the major differences between us and other primates, and aside from gross brain size, very little else of significance has been shown as most of the differences can be explained as allometric scaling. The frontal lobe, and particularly its prefrontal portion, has been a favorite target, and indeed, Brodmann (1909) claimed it was proportionally larger in humans, a view most recently championed by Deacon (1997). Unfortunately, other work has shown that the human brain has just as much frontal lobe as would be expected for a primate of its brain weight (von Bonin 1937, 1948; Semendeferi et al. 1997; Uylings and van Eden 1990), although the picture regarding prefrontal cortex has yet to be determined objectively using cytoarchitectonic criteria, which is how prefrontal cortex is differentiated from the pure motor cortex behind it (Schenker et al. 2010; Sherwood et al. 2003; Rilling et al. 2008). Hominid brain endocasts do not, alas, provide any sulcal landmarks with enough reliability to determine the boundaries of prefrontal cortex, which is so important to impulse control, and higher cognitive functions such as planning and abstraction and recognition of social actors and behavioral elements suggesting “theory of mind” abilities. Thus, these regions cannot be accurately measured in a phylogenetic sequence. However, given the apparent closeness between us and the great apes in terms of percentage of prefrontal cortex, it strikes this writer as extremely doubtful that there could be any major quantitative differences in prefrontal relative volume among the various hominin taxa. The Neanderthals, living from about 300,000 to about 28,000 years ago, have frequently been described as having smaller frontal lobes; this is not based on objective measurements, but rather a perception that the large brow ridges on these humans were constraining frontal lobe development. Studying the Neanderthal brain endocasts and comparing them to modern humans, I have failed to see any significant difference between these two groups, and Bookstein et al. (1999) showed that their prefrontal profiles were practically indistinguishable. More recently, Pearce et al. (2013) have suggested that Neanderthal orbital size meant they had larger visual cortices and thus less parietotemporal association cortex and were thus less intelligent than modern *H. sapiens*. Unfortunately, these authors did not control for facial size which is larger in Neanderthals, nor did they bother to take into account the large degree of occipital lobe variation in those Neanderthal endocasts providing such details. There is nothing in the external morphology of Neanderthal endocasts that can pinpoint any primitive characteristics in cortical morphology; and yes, their brains *were* on average larger than ours today, but not necessarily than Upper Pleistocene

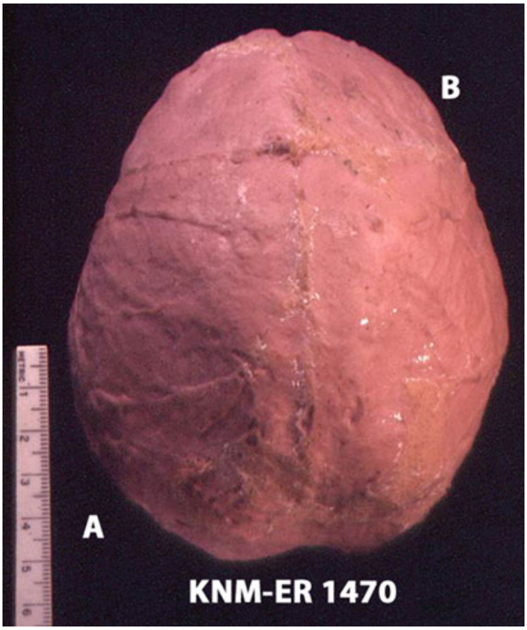

Fig. 8 Dorsal view of KNM-ER 1470, *Homo rudolfensis* (1.8 myr), showing a typical *Homo* pattern of petalias, the left occipital projecting more posterior and being wider than the right side (*A*) and the right frontal being wider than the left (*B*)

Fig. 9 Neanderthal cerebral asymmetries. *Left* is Monte Circeo and *right* is La Ferrassie. Both show a larger width of the right-frontal lobe and a larger left-occipital region (as in Fig. 8)

anatomical modern humans. Their bodies, being larger in terms of lean body mass, might have required larger brains.

Similarly, regions such as "Broca's and Wernicke's areas," anterior and posterior association cortical regions involved in motor (Broca's) and receptive (Wernicke's) aspects of speech, are determinable on most fossil endocasts, and we can determine, for example, that Broca's region is more humanlike on one brain cast of an early *Homo*, some 1.8 Ma. This is the famous KNM-ER 1470 endocast of *Homo rudolfensis* from Kenya, which had a brain volume of 752 ml. It may not be a direct ancestor to our own line of *Homo*, but it does show cerebral asymmetries similar to those found in modern *Homo* (Fig. 8, KNM-ER 1470). We know that Broca's regions in modern *Homo* are asymmetrical both in overall size and cytoarchitectonic divisions between areas 44, 45, and 47 of Brodmann (Amunts et al. 2010; Schenker et al. 2010). Interestingly, Neanderthal endocasts show similar asymmetry to modern humans in Broca's region (Fig. 9).

While the concept of reorganization has a heuristic value in directing our attention to changing quantitative relationships between different neural nuclei and fiber tracts, we cannot yet ascribe behavioral differences between closely related animals such as chimpanzee, gorilla, and orangutans or different species of the genus *Macaca* or indeed different breeds of dogs or cats with their different temperaments, aptitudes, and sociality to particular brain conformations. We simply do not know what magic level of neural description is necessary to describe species-specific behavior. Recent research on prairie and mountain voles suggests that the difference in the females' ability to retrieve pups back to the nest depends on the distribution and number of neuroreceptors for the hormone oxytocin found in several nuclei of the brain, particularly the thalamus. Otherwise, their brains appear identical (Insel and Shapiro 1992). In addition, it is necessary to remember that the brain possesses aspects of plasticity that we did not appreciate except within the past decade and that as the brain's organization unfolds ontogenetically, interactions with environmental stimuli are always occurring, and the brain builds its organization partly through its plasticity. It is difficult enough to study and understand such patterns in laboratory animals, let alone in our fossil ancestors! While the above suggests a somewhat pessimistic tone, we should remember that advances in noninvasive technology such as MRI, fMRI, PET, and tensor diffusion scanning have enormously increased our understanding of how the brain works and how neural systems integrate and dissect data from the environment, always providing us with newer paradigms for further exploration about our brains and behavior. In time, they will do the same for those of our closest relatives, the apes, in particular the bonobo and chimpanzee (see in particular Semendeferi et al. 2010).

Human Brain Asymmetry

The cerebral cortices of the human brain are usually asymmetrical and tend to grow in a torqued manner, reflecting minor differences in maturation rates. The hemispheres are seldom, if ever, equipotential in terms of functioning. Our left hemisphere is often characterized as "analytic" and involved with language tasks, while our right hemisphere appears most competent in visuospatial integration and is often thought of as the "intuitive" or "gestalt" hemisphere. These characterizations, while crude, hold up fairly accurately for right-handers and many ambidextrals. From radiographic studies, it was possible for LeMay (1976) to ascertain different petalia patterns for right- and left-handed humans with a high degree of precision. These petalias are small extensions of cerebral cortex that extend farther in one part of a hemisphere than on the other side. For example, we speak of a left-occipital right-frontal torque pattern of petalias as occurring with high frequency in right-handed individuals. This means that the left-occipital lobe bulges somewhat more posteriorly on the left hemisphere, while the right hemisphere is somewhat broader in width in the frontal lobe. In true left-handers, who make up about 8–10 % of human populations, the pattern is reversed, meaning they exhibit a right-occipital left-frontal pattern. Petalia patterns for a large collection of apes indicated that while chimpanzees, gorillas, and orangutans sometimes demonstrated asymmetries, they did not show the particular torque pattern described above *as frequently*. The gorilla, incidentally, was the most asymmetrical of the apes (Holloway and de LaCoste-Lareymondie 1982). On the other hand, brain asymmetries, particularly in the planum temporale (temporal cortex) of the chimpanzee, show a strong left-hemispheric size difference compared to the right (Gannon et al. 1998). This is simply puzzling as we do not have any evidence that chimpanzees use this structure in communication as do humans, and the fact that we share this difference with chimpanzees suggests that brain organizational features relating to complex cognitive functioning has been around for at least 5–7 myr. As our noninvasive scanning techniques become more sophisticated, we can expect to learn how these asymmetries function in animals other than ourselves. In fact, asymmetries appear in many animals and are hardly unique to primates (Hopkins and his colleagues have been in the forefront in demonstrating chimpanzee asymmetries and possible handedness: Hopkins and Nir 2010, Gomez-Robles et al. 2013, and references). It is probably the degree of asymmetry which is important in distinguishing humans from other primates (Balzeau and Gilissen 2010; Balzeau et al. 2012). Wey et al. (2013) have recently shown that intrinsic connectivity networks are more complex with regard to asymmetry of frontoparietal connectivity in humans compared to nonhuman primates. These connections probably, in part at least, account for the usual petalial asymmetries that appear more frequently in human brains.

Hominid brain endocasts, when complete for both sides (unfortunately, this is very rare), allow the paleoneurologist to assess the cerebral asymmetries, and indeed, even australopithecines appear to show beginnings of the right-handed torque pattern found in humans, and, as one progresses through time, the petalia patterns become more accentuated in the modern human direction. If we add to these observations those of Toth's (1985) studies on the early stone tools (chapters "▶ Overview of Paleolithic Archaeology," Vol. 3 and "▶ Modeling the Past: Archaeology," Vol. 1) of about 2 myr, which strongly suggest right-handedness, this underlines the fact that our early ancestors' brains, despite their small sizes (sometimes within extant apes ranges), were reorganized and that they probably had some modes of cognition very similar to our own (chapters "▶ Overview of Paleolithic Archaeology," Vol. 3 and "▶ Modeling the Past: Archaeology," Vol. 1).

Synthesis: Putting Together Size, Organization, and Asymmetry During Human Evolution

As mentioned earlier, human brain evolution has clearly been a process of integrating neurogenomic processes that led to increased size of the brain (hyperplasia and hypertrophy), and these neurogenomic changes also played roles in the reorganization (quantitative shifts) of neural nuclei, fiber tracts, and cortical cytoarchitectonics. In addition, it is probable that other changes occurred at the neurochemical level, involving neurotransmitters and receptor sites, but these are not well known from the comparative record, let alone the fossil one. This integration was sometimes gradual, sometimes "punctuated," at least based on the fossil hominid record currently available. The only reliable evidence from paleoneurology suggests that Brodmann area 17 (PVC) was reduced early in hominid evolution, signs of the reduction being clear in *A. afarensis* some 3–3.5 myr. While this would have meant a relative increase in posterior parietal cortex (area 39) and peri- and parastriate cortex (areas 18 and 19, respectively), the faithfulness of sulcal impressions does not allow for unambiguous definition of these areas. Similarly, it is not possible at this time to measure and delineate remaining areas of the temporal cortex and superior parietal lobule unambiguously. What is suggested, however, is that visuospatial abilities were most probably cognitively enhanced early in hominid evolution. It is not until we come to *H. rudolfensis* ca. 1.8 Ma that a case can be made for some frontal lobe reorganization in the third inferior frontal convolution, Broca's area. Thus, it would appear there was a gradient of cerebral reorganizational changes starting posteriorly and progressing anteriorly. Table 4 outlines these changes.

More recently, Falk et al. (2012) have argued that the Taung *A. africanus* specimen possessed an open metopic suture that allowed the prefrontal lobe to expand and widen despite the pelvic constraints thought to exist for this species in relation to bipedal locomotion. These authors then expanded this idea to several of

Table 4 Summary of reorganizational changes in the evolution of the human brain

Brain changes, reorganizational	Taxon
1. Reduction of primary visual striate cortex, area 17, and a relative increase in posterior parietal and temporal cortex, Brodmann areas 37, 39, 40, as well as 5 and 7	*Australopithecus afarensis* and *Australopithecus africanus*
2. Reorganization of frontal lobe (3rd inferior frontal convolution, Broca's areas 44,45, 47)	*Homo rudolfensis* and early *Homo*
3. Cerebral asymmetries, left-occipital right-frontal petalias	Australopithecines and early *Homo*
4. Refinements in cortical organization to a modern *Homo sapiens* pattern	*Homo erectus* to present

Source: Holloway 1997. Note: (4) is inferred, as brain endocasts cannot provide that level of detail necessary to demonstrate the refinements in cortical organization from surface features alone. Areas 18 and 19 are peri- and parastriate cortex just anterior to area 17 and are included in posterior association cortex here

Table 5 Brain size changes in hominid evolution

Brain changes	Taxon	Time (myr)	Evidence
1. Small increase, allometric[a]	*A. afarensis* to *A. africanus*	3.5–2.5	Brain endocast increase from ca. 400 to 450 + ml
2. Major increase, rapid, both allometric and non-allometric	*A. africanus* to *H. habilis*, *H. rudolfensis*	2.5–1.8	KNM–1470, 752 ml (300 ml increase)
3. Modest allometric increase in brain size to 800–1,000 ml	*H. habilis* to *H. erectus*	1.8–0.5	*H. erectus* brain endocasts and postcranial bones
4. Gradual and modest size increase to archaic non-allometric FOXP2	*H. erectus* to *H. sapiens neanderthalensis*	0.5–0.075	Archaic *H. sapiens*, Neanderthal endocasts 1,200–1,700 + ml
5. Small reduction in brain size among modern allometric	*H. sapiens* *H. sapiens sapiens*	0.015–present	Modern endocranial volumes

Source: Holloway 1997 and more recent endocast data Holloway et al. 2004
[a]Related to increase in body size only

the specimens regarded as early *Homo*, without providing any detailed evidence. Unfortunately, a newer study using micro-CT scanning (rather than medical CT scans) failed to show any evidence of a metopic suture except for a possible small portion just superior to nasion (Holloway et al. 2013), strongly suggesting that the infant metopic suture had already fused from nasion to bregma.

Table 5 outlines the major size changes in the human brain during its evolutionary odyssey. Paleoneurological data simply are not detailed enough to integrate the two tables of size and reorganizational changes into one holistic sequence of events. Basically, the paleontological record supports an early reorganizational change resulting in an increase in posterior cortex associated with visuospatial processing, perhaps accompanied by a relative small allometric increase in brain size from *A. afarensis* to *A. africanus*. This would correlate well with geological and paleontological evidence that shows that early hominids were expanding their ecological niches (chapter "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1) and becoming more diverse in their subsistence patterns in mixed habitats. We know this based on the fact that stone tool types are becoming standardized in form, tool inventories grow larger, and right-handedness is highly probable. With the advent of *Homo*, we find strong evidence for a major increase in brain size, both allometric (related to body size) and non-allometric, and a reorganized frontal lobe, broader and showing a more modern humanlike Broca's area. This suggests that there had indeed been some strong and dramatic selection pressures for a somewhat different style of sociality, one perhaps based on a primitive proto-language that had some arbitrary symboling elements, as suggested by the standardization of stone tools (e.g., Acheulean hand axes) (chapter "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3) that suggest social cohesion and control mediated through symbolically based communication (Holloway 1981). Needless to say, this is only one speculative account of the evidence. But from about 1.8 to roughly 0.5 myr, we think there were minor allometric brain size increases to the earliest *Homo erectus* hominids of Indonesia and China, where brain sizes ranged from 750 to 1,250 ml in volume. We have very little evidence for body sizes, but we believe, on the basis of the KNM-WT 15,000 Nariokotome youth from Kenya at ca. 1.6 myr, that these did not differ significantly from our own.

This is also a time during which cerebral asymmetries are becoming more strongly pronounced. With the advent of Archaic *H. sapiens*, about 0.15–0.2 myr, we find brain sizes well within modern human values and no evidence for further allometric increases, except possibly for the Neanderthals, in which it can be argued that larger brain and body sizes (lean body mass: bone and muscle) were adaptations to colder conditions. If further changes took place in cerebral and/or subcortical organization, they are simply not apparent from a paleoneurological perspective. Yet the Upper Paleolithic is the time when cave art makes its appearance, and one cannot help but wonder whether the explicit use of art involving symbolization might not also have been the time for the emergence of full language (see, e.g., Klein 2009). However, there is nothing in the direct fossil evidence, and in particular paleoneurology, to provide any evidence for such views. Claims for a single mutation are extremely speculative, and while some genes have been identified (chapters "▶ Genetics and Paleoanthropology," Vol. 1 and "▶ *Homo ergaster* and Its Contemporaries," Vol. 3) such as the FOXP2 (also in Neanderthals), these also involve more general aspects of cognition. It is more likely that stone tool making and its underlying cognitive elements are very similar to language, if not partially homologous (Holloway 1969, 1981, 2012; Stout 2006). Finally, it would appear that there has actually been a small reduction in brain size, probably allometric in nature, from about 0.015 myr to the present (Henneberg 1988; Hawks 2012).

The totality of evidence shows that the brain has always been evolving during our evolutionary journey, with myriad changes taking place at different tempos during different times. As suggested recently (Holloway 1997, p. 200):

> In sum, the major underlying selectional pressures for the evolution of the human brain were mostly social. It was an extraordinary evolutionary 'decision' to go with an animal that would take longer to mature, reach sexual maturity later, and be dependent for its food and safety upon its caretakers (parents?) for a longer period of time. The benefits for the animal were many, including a longer learning period, a more advanced, larger, and longer-growing brain, and an increasing dependence on social cohesion and tool making and tool using to cope with the environments that they encountered. Needless to say, language abilities using arbitrary symbol systems were an important ingredient in this evolution.
>
> The fossil record shows us that there was a feedback between the complexity of stone tools (which must be seen as a part of social behavior) and increasing brain size and the expansion of ecological niches. The 'initial kick,' however, the process that got the ball rolling, was a neuroendocrinological change affecting regulatory genes and target tissue-hormonal interactions that caused delayed maturation of the brain and a longer growing period, during which learning became one of our most important adaptations.

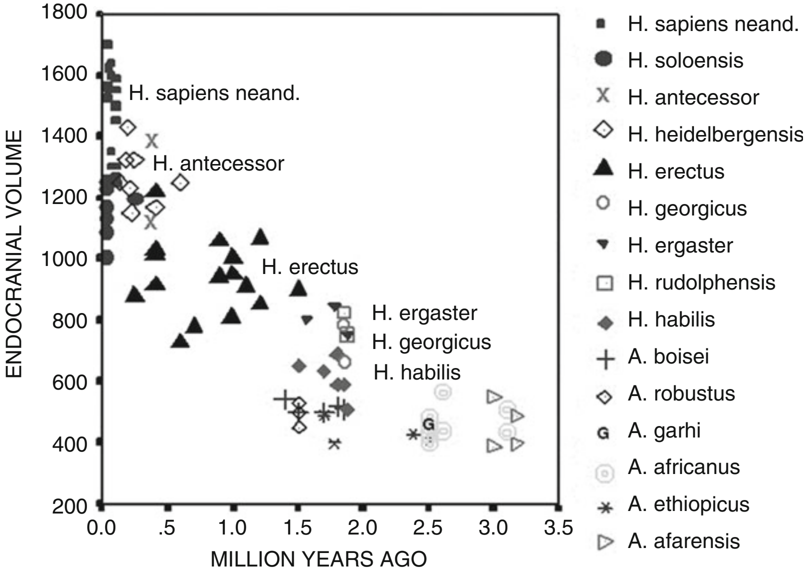

Fig. 10 Endocranial volume plotted against time, showing an accelerated change in volume from *Homo erectus* on to anatomically modern *Homo* in the late Pleistocene. This figure cannot include times of reorganization events, changes in neurogenomic elements, or any of the finer-grained differences in morphology of the endocasts. It is important to observe overlap of endocranial volumes, as well as their variation within taxa

These ideas have been detailed elsewhere (Holloway 1967, 1969, 1980, 1996, 2010), where more details may be found.

Finally, Fig. 10 provides the often-seen relationship between time and endocranial volume, and as should be apparent, there is considerable overlap between fossil groups and considerable variation within each taxon (e.g., *H. erectus*). Needless to say, such depictions cannot reveal the complex interactions between phases of reorganization, size increases through hypertrophy and hyperplasia, asymmetries in between left and right sides, different distributions of neuroreceptors and neurotransmitters, and the intricate interactions between natural selection, environmental challenges, mutation, drift, sensorimotor adaptations (think of the challenges of becoming fully bipedal), social behavior, communication skills, emotions, etc., all of which were operating during the whole of hominid brain evolution, each having some necessary relationship to neural reorganization, both cortical and subcortical. I hope the point is obvious that while we have learned much over the last century from the fossil, comparative, and neurogenomic evidence, we remain almost totally ignorant of how it really happened.

And to the Future?

There appear to be two common presumptions about our future brain evolution. One is that our biological evolution has stopped. The second is that our brains will continue to grow in size, with bulging frontal lobes, to handle our growing dependence on technology. What we have witnessed from the past fossil record is that our brains and bodies work largely in allometric fashion, and given the high metabolic cost of operating bigger brains (about 20–25 % of our metabolic resources go to supporting our brains, which constitute only 2 % of our total body weight), the second scenario seems highly unlikely. To demonstrate the first scenario would require vast amounts of information from each generation of many living populations: feasible perhaps, but not currently being collected. Furthermore, it is quite controversial whether brain size has any close relationship to intelligence; however, intelligence is actually defined and measured. Recent research based on MRI determinations of brain volume and selected batteries of cognitive tests have shown correlations between test scores and brain volume ranging from 0.4 to 0.6 (Andreasen et al. 1993; Anderson 2003; Davies et al. 2011). Most recently, Burgaleta et al. (2013) have found significant relationships between Full Scale, Performance, and Verbal IQ scores and cortical thickness in their study of cortical thickness development in children and adolescents. As more sophisticated imaging and neurogenomic advances are made, it would appear that our genes and epigenomic processes have much to do with brain biology and function. But if protein resources were to nosedive throughout the world for a significant period of time, selection would probably favor smaller body sizes in our species, and that could result in smaller brains, given an allometric relationship of roughly 0.3 between stature and brain size, at least in males (Holloway 1980). While genetic engineering may well provide some respite from the correlation between the ever-increasing mass of humanity and ecological and nutritive degradation, this too is likely to be nothing more than short-term fending off of the unstoppable future. These degradations are part and parcel of the human brain's capacity to ignore warnings that should properly curtail greed and stupidity. The paleontological record for most mammals suggests that genera (such as *Pan*, *Homo*, *Canis*, *Notocherus*, etc.) typically span approximately 5–10 Ma. Our genus has thus far a duration of about 2 myr. We, as a genus, despite our largish highly encephalized brains, have another 3 myr to go if we wish to be as successful in the paleontological longevity game.

Conclusions

Minor controversies notwithstanding, the evolution of the human brain has been an intermingled composite of allometric and non-allometric increases of brain volume and reorganizational events such as the reduction of primary visual cortex and a relative increase in both posterior association and (most probably) prefrontal cortex, as well as increased cerebral asymmetries, including Broca's and Wernicke's regions, with some of these changes already occurring in australopithecine times. As outlined in Holloway (1967), positive feedback (amplification deviation) has been a major mechanism in size increases. Exactly how this mélange of organs evolved will require many more paleontological discoveries with relatively intact crania, an unraveling of the genetic bases for both brain structures and their relationship to behaviors, and a far more complete picture of how the brain varies between male and female and among different populations throughout the world. After all, the human brain is still evolving, but for how long is quite uncertain.

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Analyzing Hominin Phylogeny: Cladistic Approach

David Strait, Frederick E. Grine, and John G. Fleagle

Contents

D. Strait (✉)
Department of Anthropology, University at Albany, Albany, NY, USA
e-mail: dstrait@albany.edu

F.E. Grine
Department of Anthropology, State University of New York, Stony Brook, NY, USA

Department of Anatomical Sciences, Stony Brook University, School of Medicine, Stony Brook, NY, USA
e-mail: fgrine@notes.cc.sunysb.edul

J.G. Fleagle
Department of Anatomical Sciences, Stony Brook University, School of Medicine, Stony Brook, NY, USA
e-mail: john.fleagle@stonybrook.edu; jfleagle@notes.cc.sunysb.edu

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Abstract

An understanding of the phylogenetic relationships among organisms is critical for evaluating the evolutionary history of their adaptations and biogeography as well as forming the basis for systematics. As the numbers of hominin fossils and hominin taxa have increased over the past 40 years, controversies over phylogeny have expanded and have become a hallmark of paleoanthropology. Concordant with the rise in taxonomic diversity, the increased use of phylogenetic systematics, or cladistics, has provided a valuable tool for reconstructing hominin phylogeny. Despite the widespread view that hominin phylogeny is a source of endless debate, there is a broad consensus regarding many aspects of hominin phylogeny.

Introduction

Phylogeny is central to our understanding of virtually any aspect of an organism's biology. An appreciation of the phylogenetic relationships of an organism not only provides a perspective on its place in the history of life and a basis for taxonomy but is also critical for evaluating biogeography as well as ecology and behavior. The adaptations of all organisms, even those as adaptively flexible as primates, are inherited, and thus any proper statistical analysis of physiological adaptations requires a consideration of phylogeny (Harvey and Pagel 1991; Purvis and Webster 1999).

In paleoanthropology at the beginning of the twenty-first century, the study of phylogeny hardly needs to be justified. The first questions that are asked about any new fossil discovery are "How is it related to us?" and "What does it tell us about our evolutionary past?" Paleoanthropology has a reputation in the popular press as a discipline characterized by disagreements over phylogeny, and this is perhaps not unfair if one considers the seemingly diverse array of phylogenetic hypotheses that have been proposed in the last two decades (Delson 1986; Walker et al. 1986; Chamberlain and Wood 1987; Grine 1988; Kimbel et al. 1988, 2004; Wood 1988, 1991, 1992; Skelton and McHenry 1992, 1998; White et al. 1994; Leakey et al. 1995, 2001; Brunet et al. 1996, 2002; Lieberman et al. 1996; Strait et al. 1997; Strait and Grine 1998, 1999, 2001, 2004; Asfaw et al. 1999; Senut et al. 2001; Martinón-Torres et al. 2007; Berger et al. 2010; Organ et al. 2011). Certainly much of the current interest in hominin phylogeny has been fueled by new paleontological discoveries. Nine new early hominid species have been described in the decades between 1994 and 2014 (White et al. 1994; Leakey et al. 1995, 2001; Brunet et al. 1996, 2002; Asfaw et al. 1999; Senut et al. 2001; Haile-Selassie et al. 2004; Berger et al. 2010). Many of these discoveries have been accompanied by phylogenetic hypotheses, not all of which are compatible with each other. However, the current importance of phylogeny in paleoanthropology and the current understanding of hominin phylogeny are not just the result of new fossil discoveries. They also reflect major theoretical and methodological advances in the discipline during recent decades (Tattersall 1999). Thus, before discussing current views on hominin phylogeny, a brief history of this endeavor during the last century is provided. The term hominin is used to mean taxa that are more closely related to humans than to any other primate.

Phylogenetic Diversity in Hominin Evolution

As numerous authors have emphasized, theoretical approaches to hominin phylogeny changed considerably through the course of the twentieth century (Fleagle and Jungers 1982; Tattersall 1999; Gundling 2005). In the early decades, discussions of hominin phylogeny were largely limited to evaluating whether the few fossil taxa that were known at the time – *Pithecanthropus erectus* from Java, *Cyphanthropus rhodesiensis*, or Rhodesian Man from Africa, Piltdown (*Eoanthropus dawsoni*) from England, Neanderthals from Europe, and, after 1925, *Australopithecus* and allied forms from Africa – were ancestral to living humans in their various forms. Two distinct issues dominated the literature. First, were any of the various fossil forms directly in the lineage leading to modern humans? As noted by Dobzhansky in 1944, most authorities found that all fossils had features which precluded placing them directly in human ancestry so that phylogenetic trees generally show a main trunk leading from somewhere in the primate past to modern humans, with each fossil taxon occupying a side branch leading to extinction (Fig. 1; Dobzhansky 1944; Tattersall 1999). Despite the lack of reliable estimates of the geological age of any extinct taxa, they were generally suggested to have branched from the (main) human lineage at different times, such that each documented some aspect of human ancestry. However, all discussion concerned the relationship of the extinct taxa to the main human lineage, with little discussion of the relationships among the extinct taxa themselves. The notable exception to this was Weidenreich's trellis model of hominin evolution in which all living and extinct taxa were interconnected but with temporal and geographic differentiation (Weidenreich 1946; Smith 1997). To a large degree, these trees showing humans at the crown just reflect the fact that in the early part of the twentieth century, as today, paleoanthropology was different from other aspects of zoology in being by definition focused primarily on tracing the history of a single organism, humans, rather than on the interrelationships of a large group of more or less equally important taxa. After all, it is the human species that writes the books.

However, as Gundling (2005) has argued, a related but distinct and in many cases more important issue in the first half of the twentieth century was the taxonomic issue of whether the various extinct species were hominins or apes. That is, where should the ape-human boundary be drawn? In most cases, these two approaches yielded concordant views. Fossils that were placed on the ape lineage were clearly not hominins. However, in some cases fossil taxa might be considered offshoots of the main human stem but still considered apes because they lacked the critical hominin character. This was at the heart of much of the debate regarding the place of Piltdown and *Australopithecus* in hominin phylogeny during the early part of the twentieth century. In general, most researchers limited the human family to modern people.

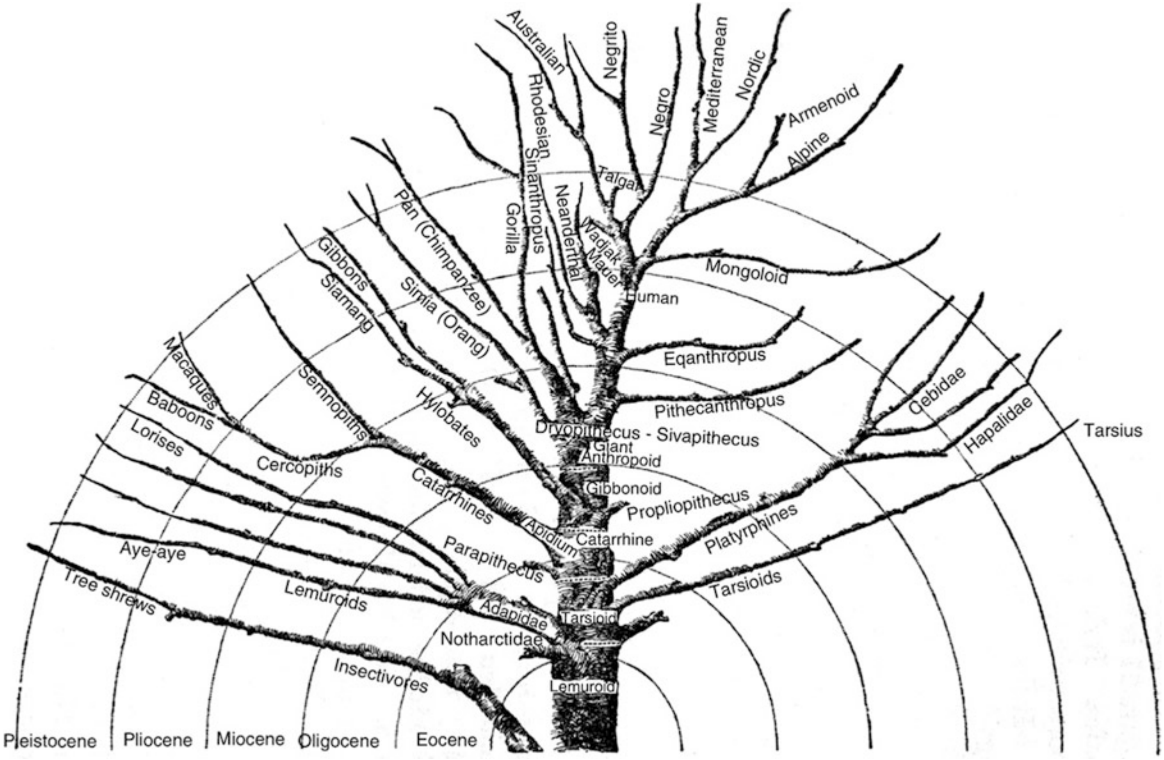

Fig. 1 A phylogeny of Primates from Hooton (1931) showing a tree with human races at the crown and the few known fossil taxa as long side branches from the main stem

As Tattersall (1999) has so eloquently discussed, all of this changed in mid-century as paleoanthropologists began, however slowly, to adopt the tenets of the New Darwinian Synthesis. Despite a growing record of new fossils, human evolution was increasingly seen as a unilinear progression through time, with all morphological diversity consigned to intraspecific variation due to geography or sexual dimorphism (Buettner-Janusch 1966; Brace 1967). All of the divergent branches from earlier in the century were incorporated into the main stem, and human evolution was seen as one continuous chain of forms separated mainly by time. The most extreme expression of this approach was Mayr's (1950) inclusion of all fossil hominins (including "robust" and "gracile australopithecines") into a single genus, *Homo*, with three species. Certainly there were other views, for example, Robinson, following Broom, repeatedly argued that *Paranthropus* was a separate lineage of hominin from *Australopithecus* and *Homo*, and Louis Leakey argued from time to time that the ancestry of the human lineage was not to be found among known fossils of the time. However, for much of the discipline, there was little appreciation of phyletic diversity in human evolution (Fig. 2). This view of limited phyletic diversity was very compelling. It was supported by the leading authorities on evolutionary biology at the time, such as Mayr and Dobzhansky; it brought paleoanthropology in line with the rest of evolutionary biology; and it conformed well with what is seen in the world today: a single species of humans with considerable intraspecific variation. Moreover, there were theoretical reasons offered to justify a lack of phyletic diversity in a culture-bearing creature (Mayr 1950; Wolpoff 1971). And while extrapolating human behavior backward into the fossil record may not be totally justified, especially for the Pliocene, it is not totally unreasonable.

However, by the 1970s the unilinear view of human evolution was being seriously challenged on several fronts and had become increasingly difficult or even impossible to support. There were clearly two distinct hominin lineages present in the Late Pliocene and Early Pleistocene at Olduvai Gorge and Koobi Fora (Leakey and Walker 1976), and there was increasing evidence that in other parts of the world modern humans had preceded or were contemporary with European Neanderthals (Leakey 1969; Stringer 1974, 1978; Howells 1975; Bräuer 1982). Likewise, "new" analytical approaches emphasized the view that morphological changes over the past 3 Myr or so did not follow a simple temporal pattern of increasingly modern features through time (Eldredge and Tattersall 1975). With an increasing number of contemporaneous taxa, the potential phylogenetic complexity of the hominin fossil record continued to grow and came to a head with the description of *Australopithecus afarensis* (hereafter called *Praeanthropus afarensis*) in 1978 and the ensuing debate over taxonomic diversity and phylogenetic relationships in early hominin evolution (Johanson et al. 1978; Johanson and White 1979; Tobias 1980; Olson 1981, 1985; White et al. 1981; Rak 1983; Kimbel et al. 1984; Skelton et al. 1986). The level of debate over early hominin diversity and phylogeny was heightened even further with the discovery in Kenya of the Black Skull (KNM-WT 17000) several years later (Delson 1986; Walker et al. 1986; Grine 1988; Kimbel et al. 1988; Wood 1988). Similarly, the debate

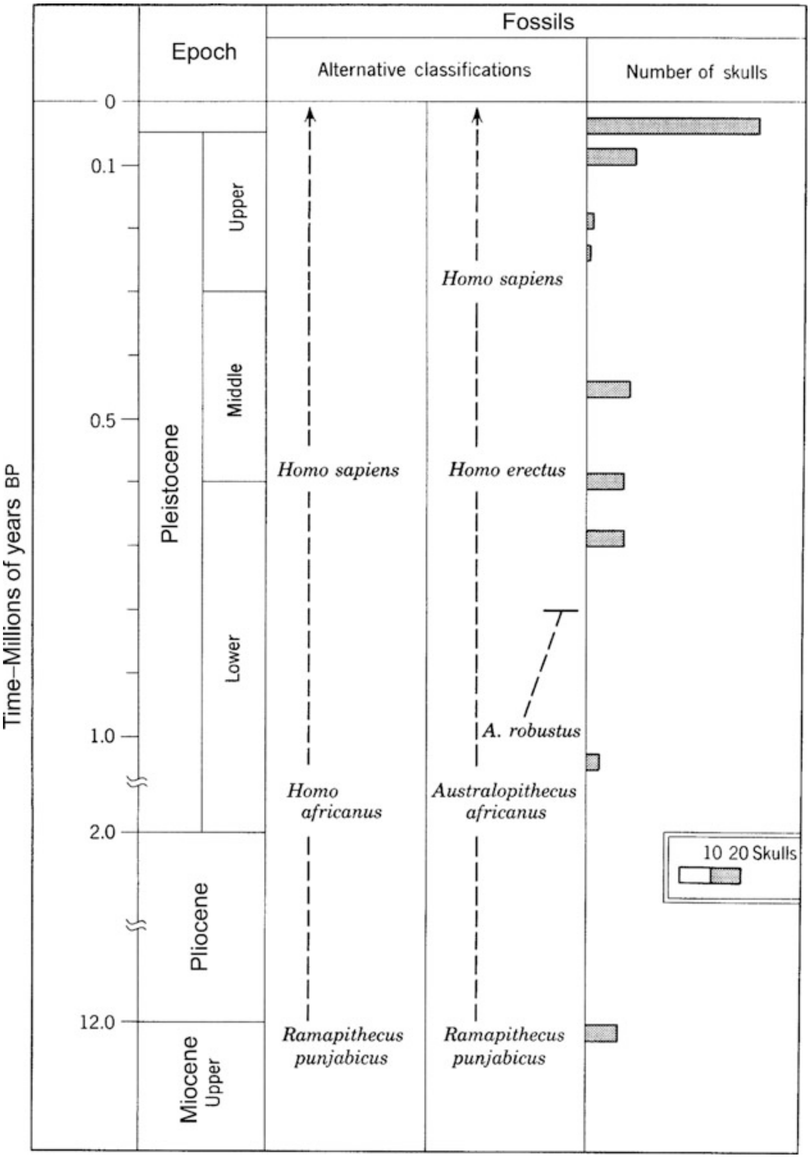

Fig. 2 A chart of hominin evolution from a major textbook from 1966 (Buettner-Janusch 1966) showing the conservative lumper's view on the *left* and the extreme splitter's view on the *right*

over the timing and geography of modern human origins and the relationship between *Homo sapiens*, Neanderthals, and *Homo erectus* expanded in the 1980s and has yet to abate (Smith and Spencer 1982; Mellars and Stringer 1989; Trinkaus 1989; Stringer 2002, 2012a).

Reconstructing Phylogeny: The Rise of Cladistics

The increasing evidence of taxonomic and phyletic diversity in hominin evolution during the 1970s and 1980s coincided with the increasing prominence of phylogenetic systematics or cladistics in paleoanthropology (Eldredge and Tattersall 1975; Luckett and Szalay 1975; Delson et al. 1977; Tattersall and Eldredge 1977; Delson 1985; Skelton et al. 1986; Wood et al. 1986; Grine et al. 1987; Grine 1988). The methods of phylogenetic systematics, or cladistics, were developed by the German entomologist Willi Hennig in 1950, but it was only with their publication in an English translation (Hennig 1966) that his methods became widely known and applied in morphological studies to understanding the phylogeny of all sorts of organisms.

Cladistics is a method of phylogenetic reconstruction premised on the notion that not all morphological similarities are indicative of phylogeny. Rather, only those similarities that are derived (i.e., novel) and inherited from a recent common ancestor should be indicative of patterns of relatedness. In practice, it is difficult (if not impossible) to discern, a priori, such features (called synapomorphies) from other types of similarities such as primitive retentions (symplesiomorphies) or traits that have evolved convergently or in parallel (homoplasies). Thus, cladistics relies on the principle of parsimony to identify synapomorphies and, hence, to reconstruct phylogeny. In a general sense, parsimony is the idea that the simplest explanation is the best one because it makes the fewest assumptions. As applied to cladistics, parsimony dictates that the best cladogram is the one that requires the fewest number of homoplasies or independent appearances of the same feature. Parsimony analysis is conventional in evolutionary biology (Kitching et al. 1998) but is viewed with skepticism by some paleoanthropologists (Trinkaus 1990; Asfaw et al. 1999; Hawks 2005). This skepticism is misplaced because, at its core, the logic of parsimony is intuitive and not too dissimilar from that of “traditional” evolutionary systematics (e.g., Olson 1981). More significantly, it provides a replicable criterion for evaluating alternative hypotheses beyond preconceived notions of how things should be (Tattersall 1996).

Consider an example in which a phylogenetic analysis is being performed on the living hominoids (*Hylobates*, *Pongo*, *Gorilla*, *Pan*, and *Homo*) and a fossil hominin (*Australopithecus*). Now consider a character with two states (knee joint valgus or varus). The nonhuman apes and various outgroup taxa (other Old World higher primates) have a varus knee, while *Homo* and *Australopithecus* have a valgus knee. Given a cladogram in which *Australopithecus* and *Homo* are sister taxa (Fig. 3a), what can be concluded about the evolution of the knee joint? There are actually many ways in which the knee joint might have evolved. It is possible that a valgus knee joint was present in all of the ancestors represented by the internal nodes of the cladogram (Fig. 3b). Such a reconstruction requires that a varus knee joint evolved in parallel in each nonhuman ape lineage. Alternatively, it is possible that a varus knee joint was present at all of the nodes of the cladogram, including the one representing the last common ancestor of hominins (Fig. 3c). This reconstruction requires that a valgus knee joint would have evolved in parallel in *Homo* and *Australopithecus*. Neither of these reconstructions is satisfying because both are

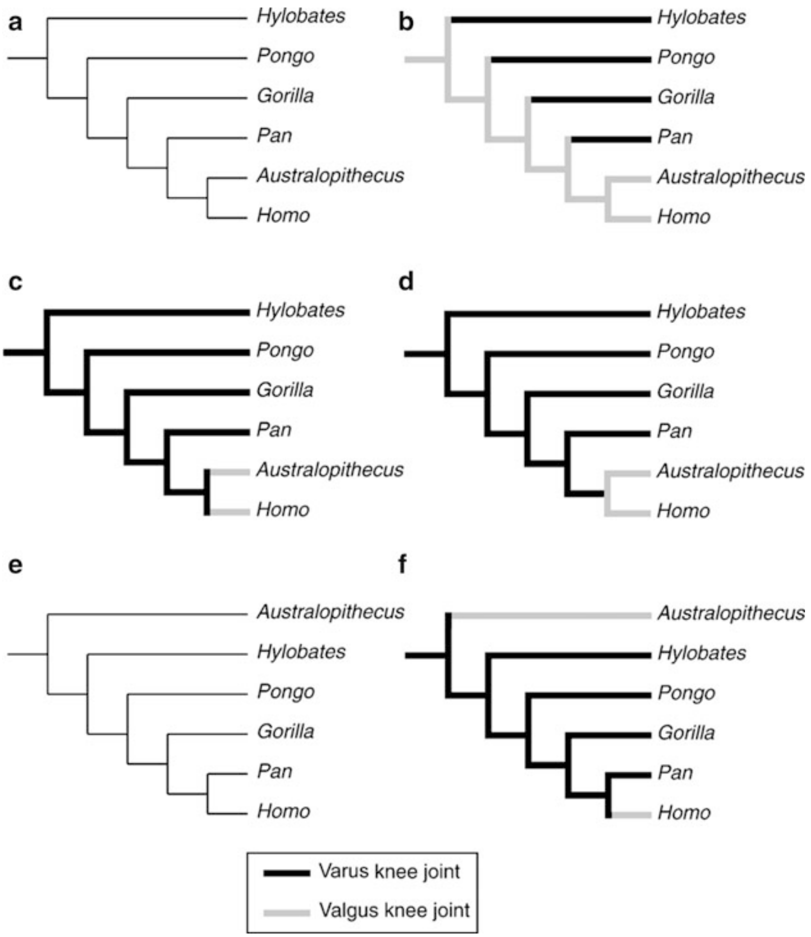

Fig. 3 Principles of cladistics. (**a**) Cladogram depicting possible phylogenetic relationships among hominoids. (**b**) Pattern of character evolution in which a varus knee evolves many times in parallel in each of the nonhuman hominoids. (**c**) Valgus knee evolves in parallel in *Homo* and *Australopithecus*. (**d**) Most parsimonious pattern of character evolution in which a valgus knee evolves once in the last common ancestor of *Australopithecus* and *Homo*. (**e**) Cladogram depicting an alternative phylogeny. (**f**) Most parsimonious pattern of character evolution in the alternative cladogram. a(=d) is preferred over (**e**) because it involves fewer changes, and it is therefore the most parsimonious

needlessly complex. There is instead a much simpler (i.e., more parsimonious) explanation for the evolution of the knee joint, namely, that a valgus knee joint evolved once in the last common ancestor of the hominins *Australopithecus* and *Homo*, who subsequently passed that trait onto its descendants (Fig. 3d). Such a reconstruction does not require any homoplasy.

Now consider an alternative cladogram in which *Australopithecus* is the sister taxon of all of the living hominoids (Fig. 3e). In this tree, the most parsimonious reconstruction of the evolution of the knee joint is one in which a valgus knee evolved in parallel in *Australopithecus* and *Homo* (Fig. 3f). No other possible reconstruction of character evolution in the knee joint requires fewer character state changes or steps. Now consider that the two cladograms presented here (Fig. 3a and e) represent alternative interpretations of hominoid phylogeny. How can these cladograms be compared so as to select one of them as the better hypothesis of phylogeny? Parsimony states that the preferred cladogram is the one that is simplest, namely, the one that minimizes the number of homoplasies required. Fewer homoplasies are required in Fig. 3d than in Fig. 3f, so the preferred cladogram is the one in which *Australopithecus* and *H. sapiens* are sister taxa (Fig. 3a). There is nothing controversial about this example, and both cladists and noncladists would agree with the result. The only difference between this example and an actual cladistic analysis is that most analyses would examine many characters at once. This is a great advantage of numerical cladistic analysis over “traditional” evolutionary systematics in which only a handful of characters tends to strongly influence the shape of phylogenetic trees. Even more significant is the fact that cladistic studies make explicit assumptions and predictions so that analyses are replicable, and the results are testable.

Cladistic Analyses of Hominin Phylogeny

Early Studies

The first cladistic analysis of hominin evolution was by Eldredge and Tattersall (1975) who also coauthored a series of papers delineating various levels of phylogeny reconstruction from producing a cladogram, to creating a phylogenetic tree, and finally an evolutionary scenario (Delson et al. 1977; Tattersall and Eldredge 1977). In the late 1970s and early 1980s, cladistic analyses in paleoanthropology were relatively simple and often consisted of little more than producing a cladogram and identifying a few shared derived characters at each node (Olson 1978; Andrews 1984; papers in Luckett and Szalay 1975; Delson 1985; Wood et al. 1986; Grine et al. 1987). Nevertheless, this was major advance from much previous work in primate phylogeny in that there was a clear effort to distinguish shared derived features from shared primitive ones, and authors provided explicit morphological justification for phylogenetic grouping at every level. Falsifying a set of relationships based on a cladistic analysis generally requires identification of additional morphological features that produce a different cladogram when analyzed. As Tattersall (1999) has pointed out, the rise of cladistics has led to a tremendous increase in the detailed documentation and analysis of hominin morphology.

The mid-1980s saw the first use of quantitative cladistic analyses in hominin evolution. By using computer algorithms researchers were able to evaluate dozens of characters and compare thousands of trees (or more), tasks that were simply unfeasible otherwise. The first efforts to evaluate hominin phylogeny using numerical methods were in an analysis of early hominin phylogeny by

Chamberlain and Wood (1987) and a study of the genus *Homo* by Stringer (1987). Numerous subsequent analyses of the phylogeny of hominins and many other groups of primates have used essentially the same methods (Fleagle and Kay 1987; Kay et al. 1997; Strait et al. 1997; Ross et al. 1998).

Moving Toward a Rough Consensus

The 1987 study of early hominin phylogeny by Chamberlain and Wood did not include *Paranthropus aethiopicus*, which subsequently became the linchpin of early hominin phylogeny. The first study to include this species was that of Wood (1988), who examined the trait list provided by Walker et al. (1986) in their description of KNM-WT 17000. Wood (1988) found that *Paranthropus robustus* and *Paranthropus boisei* are sister taxa, that *Homo* is the sister taxon of this clade, and that *Pr. afarensis*, *P. aethiopicus*, and *Australopithecus africanus* branch off in sequence from the base of the hominin tree (Fig. 4a). Notably, the three "robust" species are paraphyletic. A subsequent study by Skelton and McHenry (1992),

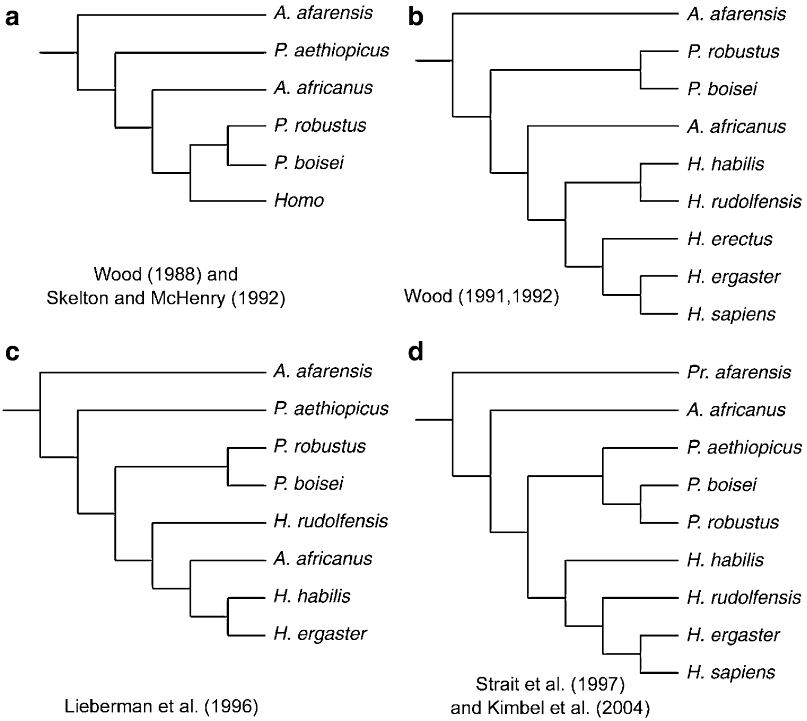

Fig. 4 Cladistic analyses of early hominins from various studies. (**a**) Cladogram of Wood (1988) and Skelton and McHenry (1992). (**b**) Cladogram of Wood (1991, 1992). (**c**) Cladogram of Lieberman et al. (1996). (**d**) Cladogram of Strait et al. (1997) and Kimbel et al. (2004)

using a more extensive trait list, found an identical cladogram. Wood (1991, 1992), using a data set composed entirely of craniometric measurements, found a most parsimonious cladogram in which *A. africanus* is the sister taxon of *Homo*, *H. habilis sensu stricto* and *H. rudolfensis* are sister taxa, and *P. boisei* and *P. robustus* are monophyletic (Fig. 4b). Technically, Wood's (1991, 1992) cladogram does not include *P. aethiopicus*, but it is reported in the text of his analysis that this species is the sister taxon of *P. boisei*. Lieberman et al. (1996) found a most parsimonious tree (Fig. 4c) in which *Paranthropus* is paraphyletic, *P. robustus* and *P. boisei* are sister taxa, and *A. africanus* is nested within the *Homo* clade. Subsequently, Strait et al. (1997) found a cladogram in which *Paranthropus* is monophyletic and the sister taxon of *Homo* (Fig. 4d). Recently, an independent analysis by Kimbel et al. (2004) has largely corroborated Strait et al.'s (1997) results. Kimbel et al. (2004) found two equally parsimonious trees: one is equivalent to those of Strait et al. (1997) and the other differs only in placing *A. africanus* as the sister taxon of the *Paranthropus* clade.

The analyses noted above appear to differ from each other, but in fact they are similar to a much greater degree than is generally acknowledged. The results of Strait et al. (1997) and Kimbel et al. (2004) differ from those of Wood (1988) and Skelton and McHenry (1992) only with respect to the relationships of *P. aethiopicus*. They differ from those of Wood (1991, 1992) principally with respect to the relationships of *A. africanus*. The most parsimonious tree of Lieberman et al. (1996) differs from that of Wood (1988) and Skelton and McHenry (1992) only with respect to *A. africanus*. Thus, these cladograms disagree primarily with respect to only two taxa, *A. africanus* and *P. aethiopicus*. There are also disagreements concerning the exact relationships of *H. habilis* and *H. rudolfensis*, but all analyses that include these taxa place them at the base of the *Homo* clade. In short, it appears as if cladistic analyses of early hominins are converging on a common set of relationships. It would be an overstatement to claim that the pattern of early hominin phylogeny is known, but insofar as repeatability is a key component of any scientific result, it would appear that the broad strokes of early hominin phylogeny are perhaps better understood than commonly acknowledged.

Phylogenetic Implications of a "Golden Age" of Discovery (1994–2004)

There were many discoveries of new fossil hominin species in the decade between 1994 and 2004 (White et al. 1994; Leakey et al. 1995, 2001; Brunet et al. 1996, 2002; Asfaw et al. 1999; Senut et al. 2001; Ward et al. 2001; Haile-Selassie et al. 2004). Despite the common refrain that phylogenetic debates can be resolved by the discovery of new fossils, many of these new finds raised rather than resolved phylogenetic questions. Although most of the new discoveries were accompanied by a phylogenetic hypothesis, those hypotheses often only addressed the relationships among a few hominin taxa. Moreover, these hypotheses were potentially difficult to test using cladistic analysis because they specified ancestor-descendant relationships without specifying sister-group relationships. At the time, the remains of many of these new hominin taxa were not yet thoroughly published, and further documentation of their morphology will doubtless permit more complete analyses. However, on the basis of information available so far, one can use cladistic analysis to test many of the initial hypotheses that have been proposed because phyletic relationships imply sister-group relationships. In particular, it is an accepted principle that a species can only be an ancestor of another taxon if it is the sister species of that taxon and if its character states resemble those reconstructed as being present in the relevant internal node of a cladogram (Szalay 1977; Smith 1994; Wagner and Erwin 1995; O'Keefe and Sander 1999). Accordingly, the phyletic hypotheses that have been proposed for many recent fossil discoveries in hominin evolution can be evaluated through reconstruction of sister-group relationships (Fig. 5).

Strait and Grine (2004) tested many of the hypotheses generated by these new taxa. They found that the pattern of hominin phylogeny is unbalanced such that many species branch off by themselves from the base of the tree, while the top of the tree is dominated by two multispecies clades, *Homo* and *Paranthropus* (Fig. 6). *Sahelanthropus* and *Ardipithecus* are, respectively, the first two branches of the tree, with subsequent branches successively represented by *Australopithecus anamensis*, *Pr. afarensis*, *Australopithecus garhi*, and *A. africanus*. If *Kenyanthropus platyops* is a valid species, then its position within the *Homo* + *Paranthropus* clade is unresolved; it is either the sister taxon of the rest of the clade or of *Paranthropus*. Relationships within *Paranthropus* are also unresolved, with *P. boisei* being the sister taxon of either *P. aethiopicus* or *P. robustus*. The position of *H. habilis* relative to *H. rudolfensis* is unresolved, but it is clear that one or the other is the basal branch of the *Homo* clade. *Homo ergaster* and *H. sapiens* are sister taxa. These results are consistent with certain of the hypotheses offered in the original descriptions and inconsistent with others.

Ardipithecus ramidus

At the time of its description (White et al. 1994), *Ardipithecus ramidus* was the oldest and most morphologically primitive hominin species then known. White et al. (1994) suggested that *Ar. ramidus* lies near the ancestry of all other hominins and that it may be the actual ancestor of those species. A cladogram consistent with this hypothesis would place *Ar. ramidus* as the sister taxon of a clade that includes all other hominin species (Fig. 5a). Strait and Grine (2004) found that *Ar. ramidus* is the sister taxon of all hominins except *Sahelanthropus* (Fig. 6). These results support the hypothesis of White et al. in a general sense insofar as *Ar. ramidus* branches off near the base of the hominin tree, if not necessarily at the basal node.

Australopithecus anamensis

The following year, Leakey et al. (1995) described *Australopithecus anamensis* as a species intermediate both chronologically and morphologically between *Ar. ramidus* and *Pr. afarensis*. Leakey et al. (1995) and Ward et al. (2001) have suggested that

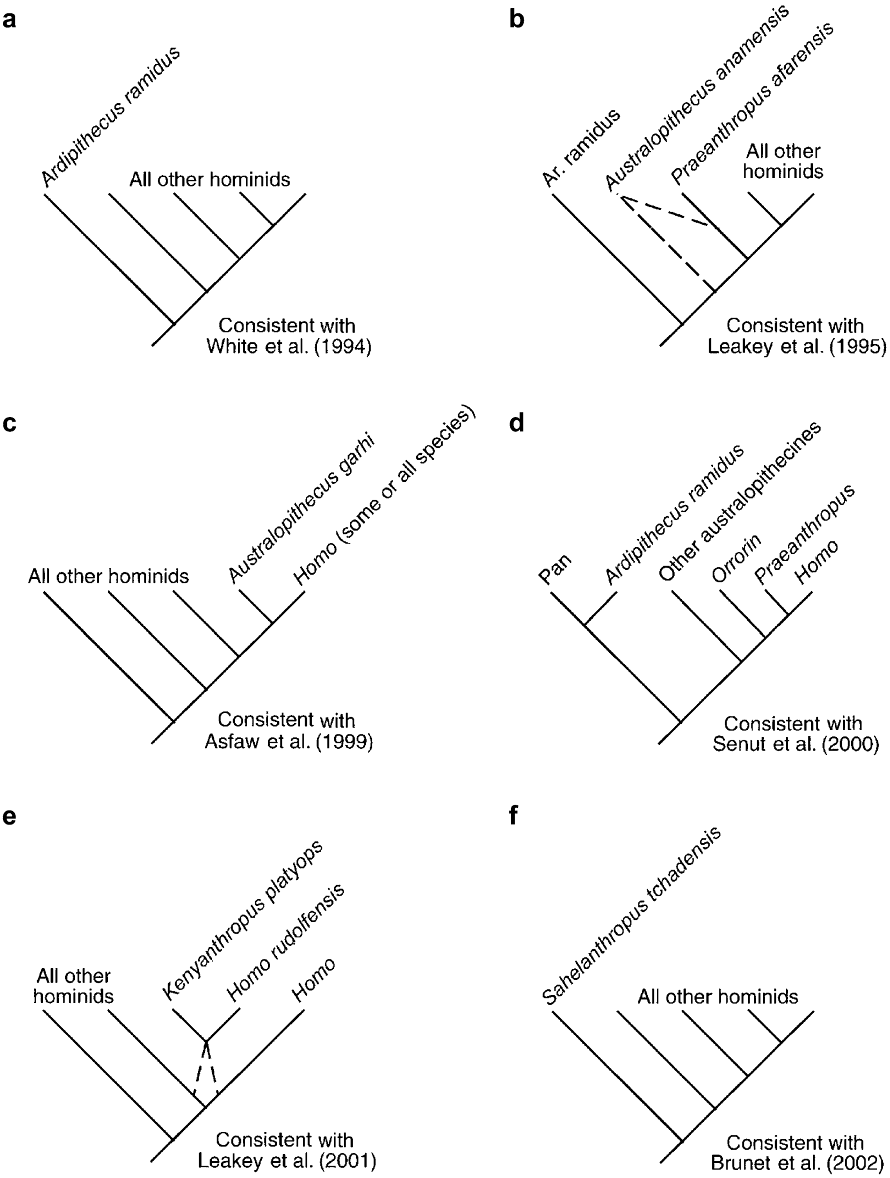

Fig. 5 Phylogenetic hypotheses associated with recently discovered hominins

A. anamensis is more closely related to later hominins than is *Ar. ramidus* and may be directly ancestral to *Pr. afarensis* (Kimbel et al., 2006). A cladogram consistent with this hypothesis would depict *A. anamensis* as diverging from a higher node on the hominin tree than *Ar. ramidus* and as the sister taxon of all later hominins (Fig. 5b). An alternative topology that might also be consistent with the phyletic hypothesis

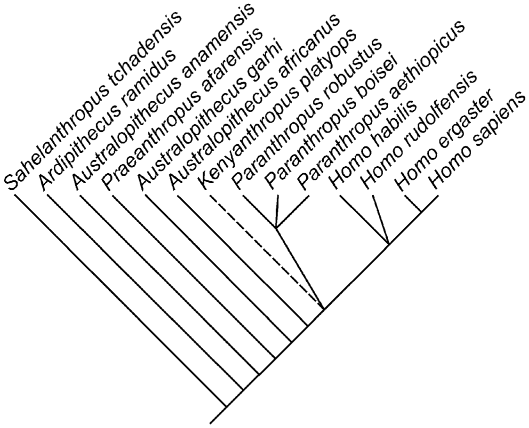

Fig. 6 Early hominin cladistic relationships found by Strait and Grine (2004)

would make *A. anamensis* the sister taxon of *Pr. afarensis*. Strait and Grine's (2004) results (Fig. 6) are consistent with the hypothesis that *A. anamensis* is the sister taxon of all hominins except *Ardipithecus* (and, presumably, *Sahelanthropus*).

Australopithecus bahrelghazali

The discovery of *Australopithecus bahrelghazali* was notable primarily because it represented the first early hominin species found in central Africa. Brunet et al. (1996) did not offer a detailed phylogenetic hypothesis for *A. bahrelghazali* but rather noted merely that the species is more derived than the contemporaneous *Pr. afarensis*. Not all workers accept that *A. bahrelghazali* and *Pr. afarensis* are distinct species (Kimbel et al. 2004). This species was not included in the analysis by Strait and Grine because it is known from only a few remains.

Australopithecus garhi

As described by Asfaw et al. (1999), *Australopithecus garhi* preserves an unexpected combination of cranial and dental characteristics. In particular, it has megadont molars and premolars but a relatively primitive-appearing face and neurocranium. Asfaw et al. (1999) implied that *A. garhi* could be a suitable ancestor for *Homo*, although they noted that the exact phylogenetic relationships of this species remained unresolved. They presented a cladogram in which *A. garhi*, *A. africanus*, *P. robustus*, *P. boisei*, *P. aethiopicus*, and *Homo* form a clade but in which relationships within that clade were left unresolved. However, they presented four phyletic trees, and in three of those, *A. garhi* was posited to be an ancestor of at least some members of the genus *Homo*. Moreover, they (Asfaw et al. 1999, p. 632) state that "If *A. garhi* proves to be the exclusive ancestor of the *Homo* clade, a cladistic classification would assign it to genus *Homo*." Such a classification would only be valid if *A. garhi* and at least some of the *Homo* species form a monophyletic group, as in Fig. 5c. Furthermore, in reference to the morphology of *A. garhi*, Asfaw et al. (1999, p. 634) state that "its lack of derived robust characters leaves it as a sister taxon to *Homo* but absent many derived *Homo* characters."

Strait and Grine's (2004) results are consistent with the hypothesis that *A. garhi* belongs to a clade that also includes *A. africanus*, *Paranthropus*, and *Homo*, insofar as *A. garhi* is reconstructed as the sister taxon of a clade comprising those taxa (Fig. 4). In addition, the relationships of *Ardipithecus ramidus*, *A. anamensis*, and *Pr. afarensis* are equivalent to those proposed by Asfaw et al. (1999). However, Asfaw et al. (1999) also suggested that *A. garhi* may be ancestral to all or part of the genus *Homo*. Cladistic analysis fails to find a sister-group relationship between *Homo* and *A. garhi* (Fig. 6). Moreover, *A. garhi* is excluded from a clade that includes only *Homo*, *Paranthropus*, *A. africanus*, and *K. platyops*. Thus, there is no support for the hypothesis that *A. garhi* and *Homo* are sister taxa, so *A. garhi* is unlikely to be the direct ancestor of *Homo*.

Orrorin tugenensis

Found in Late Miocene deposits (Senut et al. 2001), *Orrorin tugenensis* supplanted *Ar. ramidus* as the oldest known fossil hominin. Senut et al. (2001) claim that on the basis of dental and postcranial characters, *O. tugenensis* is the basal member of the *Homo* clade, to the exclusion of australopiths. Moreover, they suggest that *Ar. ramidus* is not a hominin but an ancestor of *Pan*. A cladogram consistent with these hypotheses (Fig. 5d) would have *Orrorin* and *Homo* as sister taxa, a clade of all australopithecines except *Ardipithecus* being the sister taxon of the *Orrorin* + *Praeanthropus* + *Homo* clade, and *Ardipithecus* as the sister taxon of *Pan*.

Strait and Grine's (2004) analysis did not include *Orrorin* because too few characters are preserved in that species. However, their data set can be used to examine the effect of making *Ardipithecus* the sister of *Pan* and the other australopiths monophyletic (Senut et al. 2001). The most parsimonious tree found by Strait and Grine's data set for the hypothesis that *Ardipithecus* in the sister taxon of *Pan* is 30 steps longer than that shown in Fig. 6. Considering that Senut et al.'s (2001) hypothesis is based on only a few characters (e.g., molar size, enamel thickness, details of the proximal femur), which cannot account for so many steps, it is fair to conclude that this hypothesis is not favored by cladistic analysis.

Kenyanthropus platyops

The discovery of *Kenyanthropus platyops* was notable because it demonstrated the existence of multiple hominin lineages in the Middle Pliocene. Leakey et al. (2001) noted that *Kenyanthropus platyops* appeared to share several derived character states exclusively with *H. rudolfensis*. They posited (Lieberman 2001) that this might imply that these two species had a particularly close relationship. A cladogram consistent with this hypothesis (Fig. 5e) would have *K. platyops* and *H. rudolfensis* as sister taxa. Although the validity of the species diagnosis of *Kenyanthropus platyops* has been questioned by White (2003), who has implied that many of the defining features of the type specimen are artifacts of postdepositional distortion, others have found no reason to doubt its validity.

The results of the analysis by Strait and Grine (2004) are inconsistent with the hypothesis that *K. platyops* shares especially close affinities with *H. rudolfensis* even to the point of removing the latter from the *Homo* clade. Rather, *Kenyanthropus* is the sister taxon of either *Paranthropus* or the *Homo* + *Paranthropus* clade (Fig. 6). There is no strong evidence supporting the hypothesis that *H. rudolfensis* and *K. platyops* are sister taxa, and thus the transfer of *H. rudolfensis* to the genus *Kenyanthropus* is at present unwarranted. One implication of these results is that some of the facial features shared between *H. rudolfensis* and *K. platyops* may be primitive for the *Homo* + *Paranthropus* clade, while others may be convergent. Another implication concerns the timing of early hominin cladogenic events. If *K. platyops* is a valid species, then its age (3.3–3.5 Ma) and cladistic relationships suggest that *Homo* and *Paranthropus* may have diverged from other hominin taxa up to 700 kyr prior to the earliest known specimens currently attributed to those genera (Suwa et al. 1996). It follows, therefore, that this divergence would not be explained by the Turnover Pulse Hypothesis (Vrba 1988) because the divergence would have predated the desiccations event that she postulates to have occurred in Africa between 2.7 and 2.3 Ma. These two clades may have each diversified during this period, but their origins are likely to have been earlier in the fossil record.

Sahelanthropus tchadensis

The title of "oldest hominin" now belongs to *Sahelanthropus tchadensis* (Brunet et al. 2002). Brunet et al. (2002, p. 151) note that *S. tchadensis* appears to be "the oldest and most primitive member of the hominin clade, close to the divergence of hominins and chimpanzees." The authors are cautious about the precise phylogenetic relationships of the species, but note the possibility that *Sahelanthropus* is the sister taxon of all other hominins, including *Ardipithecus*. A cladogram consistent with this hypothesis would have *Sahelanthropus* as the basal branch of the hominin clade (Fig. 5f).

Brunet et al. (2002) discuss the possibility that *Sahelanthropus* is the sister taxon of all known hominin species, including *Ardipithecus*. The Strait and Grine study is consistent with this hypothesis insofar as *Sahelanthropus* was found to be the basal branch of the hominin clade (Fig. 6). It also does not group with African apes as suggested by Wolpoff et al. (2002).

Ardipithecus kadabba

Fossils attributed to *Ardipithecus kadabba* were first assigned to a subspecies of *Ardipithecus ramidus* (Haile-Selassie 2001), but subsequent discoveries led to the elevation of this assemblage to species status (Haile-Selassie et al. 2004). The species is notable for its extremely primitive canine-premolar honing complex. Its describers imply that it is the best candidate to be the sister taxon or ancestor of all other hominins and that fossils of the other two known Miocene species, *O. tugenensis* and *S. tchadensis*, are in fact representatives of *Ar. kadabba*. This species was not included in the analysis of Strait and Grine (2004) because it is currently known from only a few body parts.

Discoveries Since 2004 and Implications for Early Hominin Relationships

The phylogenetic relationships described above collectively represent a reasonable working hypothesis of early hominin phylogeny, but more recent discoveries and descriptions of hominin fossils may necessitate important revisions in the near future. In 2009, a relatively complete skeleton of *Ar. ramidus* and other fossils from this species were comprehensively described (e.g., White et al. 2009). These descriptions confirm that *Ar. ramidus* possesses a small number of derived cranial traits that seem to place it within and near the base of the hominin clade. However, as described, the species also seems to lack nearly all of the postcranial traits traditionally associated with bipedal locomotion, as well as most of the traits seen in living apes that are functional related to suspensory locomotion. The describers of *Ar. ramidus* interpret this suite of characters to mean that the earliest hominins were not descended from an ancestor possessing suspensory traits. While possible, this hypothesis appears to be wildly unparsimonious, because it also implies that many suspensory traits must have evolved in parallel in multiple ape lineages. It is difficult to imagine cladistic analysis supporting this hypothesis but formal study is needed. Indeed, in light of the new postcranial evidence, the possibility that *Ar. ramidus* is not a hominin warrants further investigation, even if its hominin status is ultimately upheld.

In 2010, partial skeletons of a new hominin species, *Australopithecus sediba*, were discovered in southern Africa that similarly possess an unexpected mosaic of primitive and derived traits. The species exhibits craniodental traits that may align it with early *Homo*, but has postcranial characters (especially in the foot) that appear to be more primitive than those in *Pr. afarensis* (Berger et al. 2010; Zipfel et al. 2011). It has been hypothesized that it lies near the ancestry of *Homo*, but such a position might imply extensive homoplasy in hominin postcranial traits.

A difficulty in assessing the phylogenetic significance of these new data is that cladistic analyses of early hominins have traditional been based on cranial rather than postcranial characters because several early hominin species lack well-associated postcranial remains. Thus, it is difficult to quantitatively evaluate how the new postcranial data will affect parsimony-based assessments of early hominin phylogeny. Clearly, a research priority of the next decade will be to formally incorporate postcranial data into cladistic analyses of early hominins.

Phylogenetic Relationships Within the Genus *Homo*

Compared with studies of early hominin evolution in the Late Miocene and Pliocene, research on the phylogeny of Pleistocene hominins (Fig. 7) is complicated by ongoing debates on the number of species involved. The extremes range from those who, like Mayr in 1950, have argued for a single species in the genus

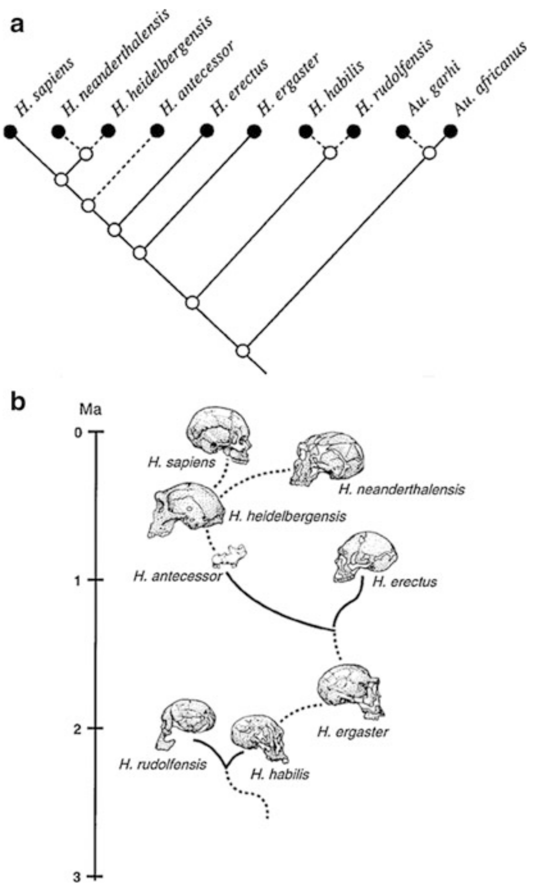

Fig. 7 Hypothetical cladogram (**a**) and phylogenetic tree (**b**) of evolution within the genus *Homo* (Modified from Tattersall 1999)

Homo (Wolpoff et al. 1994) – thus precluding any phylogeny within the genus – to others who suggest the presence of more than 15 species (Tattersall 1999). However, the majority of researchers recognize, at least for the purposes of discussion, between seven and nine species. *Homo habilis*, *Homo rudolfensis*, *Homo ergaster*, *Homo erectus*, *Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo sapiens* are widely recognized, with *Homo antecessor* and *Homo floresiensis* more poorly known and/or less widely accepted.

As noted above, the relationships of *H. habilis* and *H. rudolfensis* are poorly resolved. On the basis of an assessment of adaptive differences between *Homo* and *Australopithecus*, Wood and Collard (1999a, b) have argued that these taxa should be removed from the genus *Homo*, although their suggestion has yet to be widely adopted. Among other early Pleistocene species, there are ongoing debates over whether *Homo ergaster* from Africa is more closely related to later species of *Homo* than is the mostly Asian *Homo erectus* (e.g., Fig. 4b) or whether any of the early species of the genus *Homo* can be distinguished at all (e.g., Wood 1994; Bräuer 1994; Rightmire 1992; Lordkipanidze et al., 2013).

Like studies of early *Homo*, studies of phylogenetic relationships among later species of the genus *Homo* are bedeviled by problems of proper taxonomic allocation of fossils to be included in any analysis. Many researchers agree that the descendant of the Early Pleistocene *H. erectus* (or *H. ergaster*?) is a Middle Pleistocene taxon usually referred to as *H. heidelbergensis* (Rightmire 1998), which in turn may have given rise to both Neanderthals and modern humans (Fig. 7b). However, it has also been suggested that the immediate ancestor of *H. heidelbergensis* is not *H. erectus*, but the poorly known *H. antecessor* from the latest Early Pleistocene of Atapuerca, Spain (Bermudez de Castro et al. 2004), and possibly Italy as well (Manzi 2004). The relationships between *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* are also uncertain. Although Neanderthals have traditionally been viewed as either a subspecies or sister taxon of *H. sapiens*, many authorities now argue that *H. heidelbergensis* and *H. neanderthalensis* are sister taxa or even a single anagenetic lineage with no clear break (Arsuaga et al. 1997; Hublin 1998). From this perspective, *H. sapiens* is the sister taxon of a *H. heidelbergensis* and *H. neanderthalensis* clade (Fig. 7a). In this scheme *H. sapiens* is the descendant of a distinct early Middle Pleistocene taxon from Africa, usually given the name *Homo rhodesiensis*. Stringer (2012b) has recently argued that reconstructions of the population history of Middle Pleistocene humans might be clarified by removing the hominins from Sima de los Huesos out of *H. heidelbergensis* and instead grouping them with Neanderthals.

An interesting recent debate concerns the phylogenetic relationships of *H. floresiensis*. Although once considered to be a dwarf descendant of *Homo erectus*, there is tantalizing evidence from both cranial and postcranial anatomy suggesting that it may, in fact, represent a *H. habilis*-like hominin whose lineage pre-dates the appearance of *H. erectus* (Argue et al. 2009; Jungers et al. 2009). More study is needed, however, and this, again, speaks of the need to incorporate postcranial characters into cladistic analyses of hominins.

Conclusions

It is too soon to say whether a consensus will emerge concerning the phylogenetic relationships of the hominin species described over the last two decades, not to mention those likely to be discovered in the coming years. Strait and Grine's (2004) results on early hominin phylogeny need to be tested by other, independent cladistic analyses, and a comprehensive phylogenetic analysis of the genus *Homo* is long overdue. Postcranial characters need to be incorporated into future studies. New fossils of almost all of these species are badly needed in order to provide a better representation of characters and a better understanding of intraspecific variation. Improvements in techniques to assess character independence, morphological integration, and developmental modularity (McCollum 1999; Ackermann and Cheverud 2000; Strait 2001) will also greatly improve the accuracy of cladistic analysis. At the heart of all attempts to understand hominin phylogeny are unresolved issues regarding the identification of species in the fossil record (Tattersall 1986, 1992, 1996;

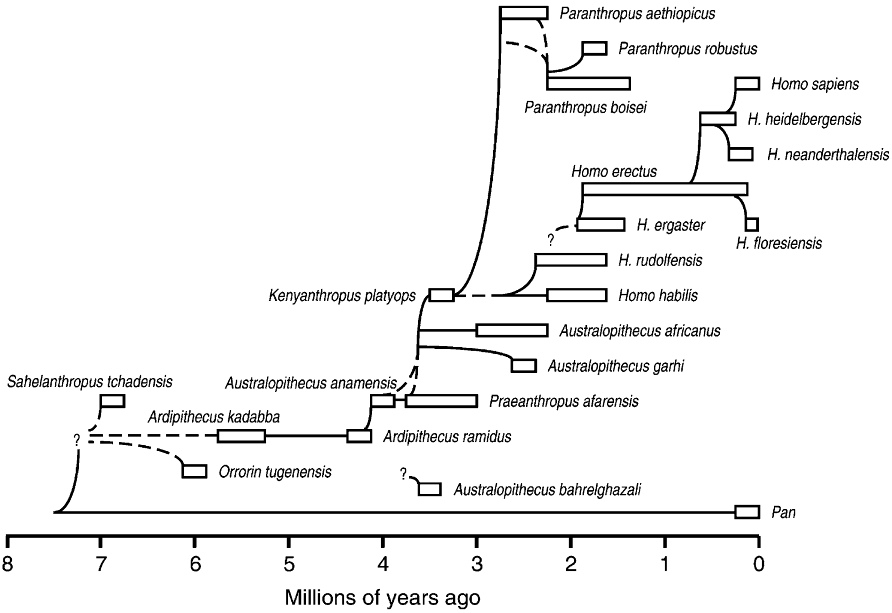

Fig. 8 A summary of the temporal span and phylogenetic relationships among fossil hominins

Kimbel and Rak 1993; Plavcan and Cope 2001). This is especially critical within the genus *Homo*, in which genetic evidence has demonstrated that population history is perhaps more complicated than might have been expected based on a consideration of the fossil record alone (Green et al. 2010; Reich et al. 2010).

Despite these caveats, a broad consensus regarding the phylogenetic relationships of many hominin taxa has emerged (Fig. 8). It is likely that disagreement will persist as to the exact relationships among *S. tchadensis*, *Ar. kadabba*, and *O. tugenensis* until they are known by more body parts that can be directly compared, but most workers accept that these species all lie somewhere near the base of the hominin tree. The greatest disagreement will probably focus on *A. garhi* and *K. platyops* and the relationships of these species to the genus *Homo*, as well as whether or not *Ar. ramidus* is a hominin. While there is broad general agreement about overall phylogenetic relationships in later hominin evolution, there is less consensus about the number of taxa that should be identified. The number and relationships of the early species of the genus *Homo* remain a source of ongoing debate (Wood and Collard 1999a, b; Wood and Lonergan 2008; Henke and Hardt 2011; Stringer 2012a), and there are various alternative interpretations concerning the few fossils from the Early and Middle Pleistocene (Tattersall 1986; Rightmire 1998; Bermudez de Castro et al. 2004; Manzi 2004).

Some have argued that hominin phylogeny will never be resolved in a timely fashion because of the many gaps in the fossil record (White 2002). That view is unduly pessimistic. Of course there are gaps in the fossil record! Despite the fact that knowledge of that record is constantly expanding, it will never be complete. That is not an excuse for failing to do the best one can with the material that is available in order to evaluate phylogenetic hypotheses. There is no doubt that the fossil record samples only a portion of the organisms, including hominins, that have ever lived and that new discoveries always document new, unanticipated aspects of evolutionary diversity. This is why paleontology is such an exciting and rewarding field of study. Despite this serendipitous sampling of the history of life, and ongoing uncertainties regarding some taxa, cladistic analysis has led researchers toward a general consensus of the phylogenetic relationship of many of the hominin taxa that can be documented and remains the best hope for resolving future questions about hominin phylogeny.

Cross-References

- ▶ General Principles of Evolutionary Morphology
- ▶ Historical Overview of Paleoanthropological Research
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Later Middle Pleistocene *Homo*
- ▶ Neanderthals and Their Contemporaries
- ▶ Paleoecology: An Adequate Window on the Past?
- ▶ Quantitative Approaches to Phylogenetics
- ▶ Quaternary Geology and Paleoenvironments
- ▶ The Earliest Putative *Homo* Fossils
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ The Species and Diversity of Australopiths

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Phylogenetic Relationships of Hominids: Biomolecular Approach

Todd R. Disotell

Contents

Abstract

Biomolecules, in particular DNA, assist us in generating and testing hypotheses about human evolutionary history. Molecular analyses testing for and then utilizing a local molecular clock can inform us as to the timing of the split between different lineages or populations. When applied to the split between hominins and chimpanzees, for instance, the molecular clock estimates of their divergence date place constraints on interpretations of the growing fossil record from the Late Miocene and Early Pliocene. The pattern and distribution of modern human variation can be used to extrapolate back in time to infer when and where the modern human gene pool arose. Mitochondrial DNA and Y chromosome sequences and markers have been extensively surveyed in populations from around the world. Numerous nuclear loci and other markers, such as microsatellites and *Alu* insertions, have similarly been sampled and analyzed. More recently, high-throughput massively parallel sequencing technologies have allowed for the characterization of hundreds of human and

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T.R. Disotell (✉)
Department of Anthropology, Center for the Study of Human Origins, New York University, New York, NY, USA
e-mail: todd.disotell@nyu.edu

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nonhuman primate complete genomes. The majority of such analyses point toward a relatively recent origin for modern human diversity from a small population in Africa within the last 200 Ka, with a subsequent dispersal into Eurasia less than 100 Ka though there is some debate as to the timing of these events. While analyses of ancient mitochondrial sequences from archaic hominins strongly suggest that archaic females did not contribute to the modern human mitochondrial gene pool, whole-genome sequences of two archaic populations suggest limited interbreeding with modern humans in Eurasia but not Africa. Analyses of modern African genomes suggest that some populations also interbred with an as yet unknown archaic population or populations. Thus, while a complete replacement of archaic populations by African-derived modern humans is no longer fully tenable, only a limited amount interbreeding between anatomically modern human populations and archaic forebears is likely to have taken place.

Introduction

Over 100 years ago, George Nuttall (1862–1937) began his book, *Blood Immunity and Blood Relationship*, with a discussion of the classification of the order Primates stating, “The persistence of the chemical blood-relationship between the various groups of animals serves to carry us back into geological times, and I believe that we have but begun the work along these lines, and that it will lead to valuable results in the study of various problems of evolution” (Nuttall 1904, p. 4).

We now know that biomolecules, in particular DNA, can inform us about phylogeny and population history, selection, and perhaps even taxonomy. Inferences drawn from molecular analyses can provide insights into at least three areas of hominin history. The first is the timing of the hominin–chimpanzee split, which in turn may provide a background for interpreting the growing Late Miocene–Early Pliocene hominin and hominid fossil record. The second is the origins of modern human populations by extrapolating into the past by examining the pattern of modern human molecular variation. Finally, Middle to Late Pleistocene fossils such as the Neanderthals and Denisovans have now successfully yielded DNA sequence information which allows us to draw inferences back to the point at which the modern and archaic lineages originated (see Fig. 1).

History

Nuttall’s research, carried out shortly after the discovery of blood groups in 1901, was based on qualitative and quantitative measures of the immunological reactions of various proteins in the blood. Immunological approaches were improved and systematically applied to questions about primate evolutionary history extensively in the 1960s through the works of Goodman (1961, 1963) and Sarich and Wilson (1966, 1967). It was also during this period that the concept of the molecular clock

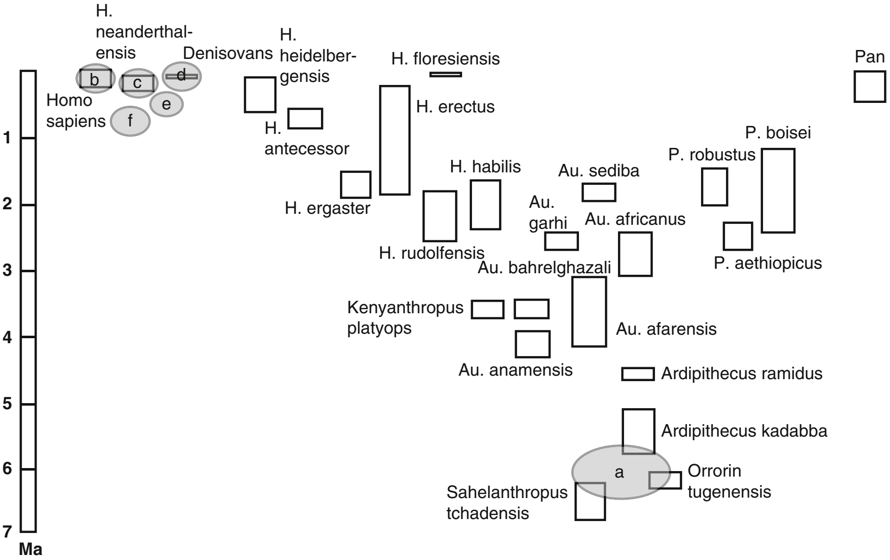

Fig. 1 Time ranges of hominin species (After Wood 2010). *Gray ovals* represent the six places where molecular information may be informative. (*a*) The timing of the split between hominins and chimpanzees, (*b*) the origins of the modern human gene pool, (*c*) the diversity and origin of the Neanderthal gene pool, (*d*) the diversity and origin of the Denisovan gene pool, (*e*) the time of divergence between Neanderthals and Denisovans, and (*f*) the time of divergence between the common ancestor of Neanderthals and Denisovans and that of modern humans

was first proposed (Zuckerkandl and Pauling 1962). By the 1970s, research increased directly at the DNA level, though only using approximate methods such as DNA–DNA hybridization and restriction mapping to measure the differences between species, populations, and individuals. This time period also saw the development of chromosomal banding techniques for evolutionary analysis (Chiarelli 1966; Dutrillaux 1979; Yunis and Prakash 1982). These techniques have been further developed and have helped us understand the rearrangements that are both shared and differ between humans and other primates using fluorescence in situ hybridization (FISH) and reciprocal chromosomal painting (Weinberg and Stanyon 1998). Chromosomal techniques are generally only used clinically within modern humans as our level of chromosomal variation is extremely low.

Techniques that directly measure differences at the DNA sequence level have advanced greatly in the last three decades. Earlier studies of species and population differences utilized restriction endonucleases, enzymes that cut a strand of DNA at a particular short sequence pattern, to estimate either genetic distances or to provide phylogenetically informative characters between individuals in the sample. Until 2005, the majority of molecular information was derived using a variety of manual to semiautomated technologies that allowed DNA sequences or microsatellite allele sizes to be relatively rapidly determined. The use of the variants of the polymerase chain reaction (PCR) allowed for minute samples from a variety of biomaterials including blood, saliva, hair, feces, bones, teeth, and other biological materials to be amplified and/or sequenced from only a few molecules of DNA. Amplification was generally followed by gel or capillary electrophoresis to determine sequences or allele sizes.

Practical constraints required the use of either relatively short sequences (hundreds to tens of thousands of bases) or variable markers such as retroelements, microsatellites, and SNPs. One popular class of molecular markers consists of retrotransposable elements, including short interspersed elements (SINEs) and long interspersed elements (LINEs). SINEs, particularly the *Alu* family, which exists in over 500,000 copies in human genomes, can vary in number and location between individuals and populations (Batzer et al. 1996). Because the absence of an *Alu* element at a particular location in the genome is the ancestral condition, the shared presence of an element is most likely indicative of common descent. Similarly, the longer LINE elements, which make up over 15 % of human genomes, can be used as markers of common evolutionary descent (Sheen et al. 2000; Boissinot and Furano 2005). Extremely variable short tandem repeats (STRs), also known as microsatellites, have also proven useful in individual identification and parentage assessment and to infer population relationships based on the analysis of the frequencies of different allele sizes (Bowcock et al. 1994). SNPs continue to be used to infer population relationships and evolutionary history (Yu et al. 2002).

Another class of genomic DNA elements is the endogenous retroviruses, which make up a surprisingly large portion of the human genome. Their type, copy number, and positions within the genome vary between populations, so they can provide useful evolutionary markers in the same way as the retrotransposable elements mentioned above (Turner et al. 2001). Extragenomic molecular data from pathogenic and commensal organisms can also be useful in inferring human evolutionary history. Tapeworm, lice, and stomach bacteria sequences have all been used to generate and test hypotheses about human population relationships and migrations (Hoberg et al. 2001; Disotell 2003; Leo and Barker 2005).

Single-nucleotide polymorphisms (SNPs) are typically characterized using DNA microarrays in which DNA probes for variants that are to be identified are usually attached to a solid surface. A DNA sample is then passed over the microarray to allow for hybridization of the source DNA to the probes which are then detected by fluorescence or chemiluminescence indicating a match. Current DNA microarrays can detect up to nearly two million SNPs, copy number variants, or other markers at once.

Beginning in 2005, several new sequencing platforms were developed that generate several orders of magnitude more data than previous methods, at dramatically reduced cost (Mardis 2013). Often referred to as Next Generation (NextGen) technologies, Second Generation (2ndGen) is probably a better term as there will always be a next generation. Though multiple platforms and methods are used, they all basically share several commonalities. First, rather than cloning or amplifying the DNA in advance, different synthetic adapters are added to the source DNA depending upon the platform used, and the fragments are amplified on a solid surface, either glass or a tiny bead, to which the adapters bind. Then the bound amplified fragments are sequenced by adding nucleotides that are detected one at a time as they are incorporated into the amplified clusters. The sequencing and detection step is carried out in a massively parallel manner so that hundreds of thousands to millions of DNA fragments are sequenced simultaneously. One downside to these techniques is that they generate relatively short sequences (from 50 to 60 to a few hundred bases long), with a relatively high error rate. These then need to be assembled into a genome or portion of a genome usually be comparing them to a closely related reference genome.

The completion of the first human genomes in 2001 by Lander et al. (2001) and Venter et al. (2001) was followed in 2005 by a complete draft of the chimpanzee and, in 2007, the macaque genomes, using conventional sequencing approaches allowing for even more sophisticated comparative analyses (Chimpanzee Sequencing and Analysis Consortium 2005; Rhesus Macaque Genome Sequencing and Analysis Consortium 2007). Second-Generation technologies were used to sequence the orangutan (Locke et al. 2011), gorilla (Scally et al. 2012), and bonobo (Prüfer et al. 2012) genomes. These genomes have not only allowed for far more in-depth analyses of the similarities and differences among the various ape lineages but provide information useful in inferring the polarities of molecular characters that vary among humans.

Finally, molecular data are being used to investigate the differences between humans and our primate relatives through studies of copy number variation, gene expression, epigenetics, and other underlying molecular and developmental processes; but these issues are beyond the scope of this review (e.g., Enard et al. 2002; Cheng et al. 2005; Eckhardt et al. 2006; Sudmant et al. 2013; Pääbo 2014).

Hominin Origins

Molecular studies have been used to draw inferences about the possible Eurasian origin of the African hominids including the ancestor of hominins, though not without controversy (Miyamoto et al. 1998; Stewart and Disotell 1998; Moyà-Solà et al. 1999; Heizmann and Begun 2001; Begun et al. 2012). However, until the discoveries of the Late Miocene hominids and/or hominins including *Ardipithecus*, *Orrorin*, and *Sahelanthropus* (Haile-Selassie 2001; Senut et al. 2001; Brunet et al. 2002), little could be said about origin of the hominin lineage itself. In fact, only its date, approximately 6 Ma, inferred from molecular clock estimates was available (Chen and Li 2001; Wildman et al. 2003). This date estimate is also not without controversy, though significantly older dates put forth by Arnason et al. (1996, 1998) and supported by Tavare et al. (2002) do not appear to be supported by more detailed molecular analyses (Raaum et al. 2005).

Recently a new debate has broken out over estimating divergence dates with molecular data. Typically, comparisons between two lineages for which good fossil evidence provides the age of at least one of them are converted into rates of change per year. This is of course dependent not only on proper placement of a fossil but also its appearance in the record near the point of divergence. Nevertheless, multiple estimates within the catarrhines have relatively consistently suggested a rate of approximately 1.0×10^{-9} bp^{-1} $year^{-1}$ (Takahata and Satta 1997; Green et al. 2010). With whole-genome analyses now common and relatively inexpensive, a direct estimation of the human mutation rate can be estimated by examining parent–offspring triads across the whole genome. With a known mutation rate and an estimate of the generation time for the taxa being investigated, divergence dates can be estimated. Coupled with new estimates of generation times for human, chimpanzees, and gorillas (Langergraber et al. 2012), an overall rate of approximately 0.5×10^{-9} bp^{-1} $year^{-1}$ or about half the previous rate has been estimated (Roach et al. 2010; 1000 Genomes Project Consortium 2010; Scally and Durbin 2012). However O'Roak et al. (2012) do not find such a slow rate in their whole-genome family triad study. Ho et al. (2011) provide an excellent discussion of the discrepancy in rates of evolution determined at different timescales, at both the morphological and molecular levels.

Fu et al. (2013) provide a third way of estimating molecular rates of evolution, at least for the mitochondrial genome. By sequencing mtDNA in fossils dated to within the last 40,000 years (the reliable range of radiocarbon dating), they can measure the effect of "branch shortening" in which fossil lineages are missing the substitutions that would have occurred had they survived to the present. The number of missing substitutions coupled with the dates of the samples provided remarkably consistent rates. These rates when applied to mitochondrial trees provide divergence estimates that fall within the range of the classically accepted dates discussed below. When high enough quality whole-genome data become available, this technique will be applied to nuclear DNA as well (Green and Shapiro 2013).

It should not come as a surprise that, with whole genomes of the apes available, the interpretation of when speciation occurred has become more complex. For instance, 15 % of the sequences in the western lowland gorilla genome are most similar to those in humans, and 15 % are most similar to those in chimpanzees despite the overall closer relationship of chimpanzees to humans (Scally et al. 2012). Furthermore, 3 % of the human genome is more closely related to chimpanzees or bonobos than they are to each other (Prüfer et al. 2012). These differences in gene lineages from the overall pattern of speciation may be due to several phenomena. In incomplete lineage sorting, ancestral polymorphism or variation in the common ancestral population may be partitioned into descendent populations and ultimately descendent species such that individual genes do not match the species phylogeny. If there is gene flow between the ancestral populations or the incipient species, the gene phylogeny may similarly differ from the species phylogeny. Thus, care must be taken in interpreting molecular divergence dates, especially those derived from concatenated datasets and whole genomes.

With the discovery of these Late Miocene fossils, numerous phylogenetic hypotheses were put forth suggesting their hominin status (Haile-Selassie 2001; Brunet et al. 2002) or that only one was an early hominin and the others were either fossil chimpanzees or gorillas or broadly ancestral to both the human and chimpanzee lineages (Senut et al. 2001). Given the vast amount of molecular data

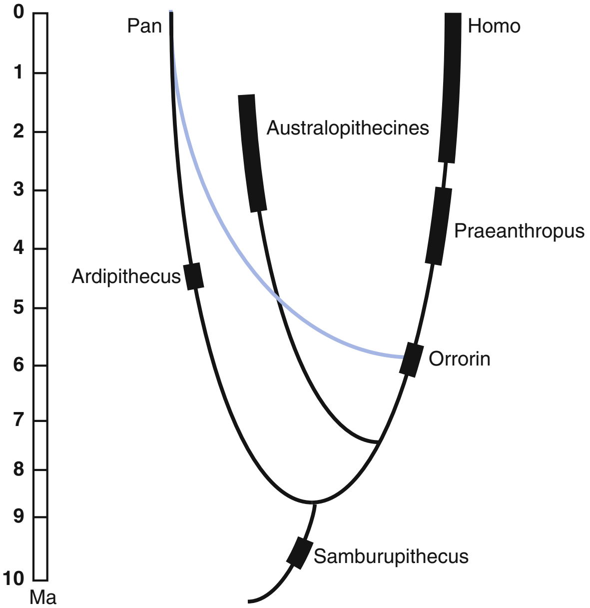

Fig. 2 Potential phylogenetic relationships of Late Miocene and Early Pliocene hominins and hominids. *Black lines* and ranges after Senut et al. (2001); *gray line* represents the molecular clock estimate of the divergence of hominins and chimpanzees (Chen and Li 2001; Wildman et al. 2003)

collected to assess the relationships among African apes including humans, "… genetic data can also give us trees that are well enough proportioned to be useful to us as paleontologists and that can provide constraints on our 'flights of fancy,' when calibrated by plausible paleontological or other historical data" (Pilbeam 1995). An approximately 6 Ma split between humans and chimpanzees (see Fig. 2), for instance, makes untenable the phylogenetic proposal put forth by Senut et al. (2001), in which *Ardipithecus* falls along the chimpanzee lineage and *Orrorin* falls well within the hominin lineage more than 2.5 Ma after a human–chimpanzee divergence (assumed by Senut et al. to have occurred around 8.5 Ma). On the other hand, if the purported much slower rate of evolution is applied, the human–chimpanzee split (and all others) becomes much older. Hawks (2012) points out that if older divergence dates are accepted, then fossils such as *Chororapithecus* at 10.5 million years old could indeed fall along the gorilla lineage as claimed by Suwa et al. (2007). The gorilla affinities of *Chororapithecus* have, however, been disputed by others (Gibbons 2007). Overall, given that the phylogenetic approach to estimating divergence dates and the method using missing substitutions from fossils concur and the whole-genome family triad methods give suspiciously ancient divergence estimates for many primate lineages, it is probably best to continue to use the faster rate estimates when inferring dates.

An interesting proposal put forth by Wildman et al. (2003) using a combination of lineage divergence estimates based both on molecular and fossil data would substantially revise the taxonomy of all hominins and our close relatives, the chimpanzees. They propose a time-based phylogenetic classification/taxonomy linking the timing of the origin of a clade to its taxonomic level for most catarrhines. In their scheme, because chimpanzees and humans share a recent common ancestor at only 6 Ma, chimpanzees would be classified within the genus *Homo* as *Homo* (*Pan*) *troglodytes* and *Homo* (*Pan*) *paniscus*. Consequently, all genera of hominins, including *Australopithecus*, *Paranthropus*, and *Kenyanthropus*, would necessarily be sunk into the genus *Homo*. Depending on their phylogenetic positions and divergence dates, *Sahelanthropus*, *Orrorin*, and *Ardipithecus* might similarly be included within *Homo*. While the chaos and difficulty of adopting this strategy are apparent, the underlying phylogenetic logic is appealing.

Modern Human Origins

Most studies of blood group allele frequencies and protein polymorphisms carried out in the 1960s and early 1970s that presented their findings in the form of a phylogenetic tree posited a basal split between Asians and an Afro-European cluster. In 1974, Nei and Roychoudury (1974) analyzed 21 blood group systems and 35 polymorphic proteins from which they inferred an initial African versus European–Asian split. In this rather prescient chapter, they extrapolated from estimated amino acid replacement rates and inferred that the basal split between Africans and Eurasians occurred approximately 120 Ka and that Europeans and Asians split around 55 Ka. Few additional studies attempting to infer modern human origins were carried out until the late 1980s.

Two seminal papers published in the late 1980s by Cann et al. (1987) and Vigilant et al. (1989), both working in Allan Wilson's laboratory at the University of California at Berkeley, inferred a less than 200 Ka African origin for all human mitochondrial DNA (mtDNA) and, by extrapolation, perhaps for all modern populations. Known by various names, the "Mitochondrial Eve" or "Out-of-Africa" hypothesis, will hereafter be referred to as the Recent African Origin (RAO) model. This model stands in contrast to the regional continuity or multiregional (MRE) model in which local populations are thought to derive from the original groups that migrated into the various regions of the Old World over 1 Ma from Africa, with various amounts of gene flow between the different regions ever since (Wolpoff et al. 2000). Cann et al.'s (1987) study was based on phylogenetic inferences drawn from parsimony analysis of high-resolution restriction mapping of the whole mtDNA genome. To counter criticisms of the precision of restriction mapping, the geographical sampling, and the lack of an outgroup in Cann et al.'s original analysis, Vigilant et al. (1989) employed one of the first uses of PCR utilizing hair samples to generate nucleotide sequences in a phylogenetic analysis, followed by a sequence-based analysis with a much larger sample size (Vigilant et al. 1991). Through sequencing the D-loop or control region of the mtDNA genome, they were able to align human sequences with those of a chimpanzee in order to carry out a parsimony analysis rooted by an outgroup. The results were remarkably congruent with those of Cann et al. (1987), in inferring a similar timing and location for the origin of all contemporary human mtDNA: approximately 200 Ka in Africa.

The initial papers of Cann et al. (1987) and Vigilant et al. (1989, 1991) came under criticism for an important analytical flaw. Their parsimony trees suggesting a recent African ancestry for all modern mtDNA were derived from heuristic search strategies that did not find the most parsimonious trees for their respective data sets. Other researchers were able to infer trees without African roots that were more parsimonious (Maddison et al. 1992; Templeton et al. 1992). Since no search strategy is available to guarantee the most parsimonious tree is found for such large data sets, alternative strategies were utilized to infer the root of the modern human mtDNA tree. However, Stoneking et al. (1992) and Sherry et al. (1994) demonstrated that the much greater amount of mtDNA diversity found within Africa compared to outside of it was best explained by a longer period of time for it to accumulate within Africa. Additional smaller data sets chosen to represent the most diverse human sequences possible were also analyzed, and an African origin for modern mtDNA types was inferred (Kocher and Wilson 1991). Additional molecular dating inferences also supported the approximately 200 Kyr time frame inferred to explain human mtDNA diversity (Ruvolo et al. 1994).

A huge number of human complete mitochondrial genome sequences has been collected and subjected to phylogenetic and population genetic analyses. Due to the rapid rate of evolution of the mtDNA genome, short sequences such as those found in the D-loop or control region are not always useful over long timescales and may show spurious clustering due to homoplasy or multiple substitutions at the same site, including saturation of substitutions at a site. One solution when available is to characterize both the fast-evolving control region and several more slowly evolving region of the mtDNA genome to define haplogroups or related lineages of mtDNA haplotypes. In fact, sequencing the complete 16.5 kb mtDNA genome has become commonplace (Ingman et al. 2000; Herrnstadt et al. 2002). By the end of 2013, more than 20,000 complete human mitochondrial genomes had been deposited in GenBank. Such analyses show more geographic partitioning of mtDNA sequences than previous studies based on much shorter sequences revealed.

Unfortunately, the nomenclature for major mtDNA lineages has developed haphazardly, mostly by time of definition and not with phylogenetic relationships in mind. In fact, most haplogroups are defined by the number of substitutions that they differ from the first complete human mtDNA sequence (a European) published (Anderson et al. 1981). A recent proposal has been put forth to redefine the mtDNA tree from its root, by inferring the common ancestral human mtDNA haplotype through analyzing 8,216 modern mitogenomes along with those from six Neanderthals (Behar et al. 2012). Seven major lineages (L0–6) have been defined for African mtDNA haplotypes, while two macro-haplogroups (M and N) contain all Eurasian lineages which are derived from African L3 (Kivisild et al. 1999; Herrnstadt et al. 2002). Sub-haplogroups of macro-haplogroup M are almost exclusively found among contemporary Asians along with a small number of individuals in Africa presumably due to back migrations (Gonzalez et al. 2007). Macro-haplogroup N contains around a dozen sub-haplogroups that are found predominantly in Europe with another seven that are found in Asia and the Americas (see Fig. 3).

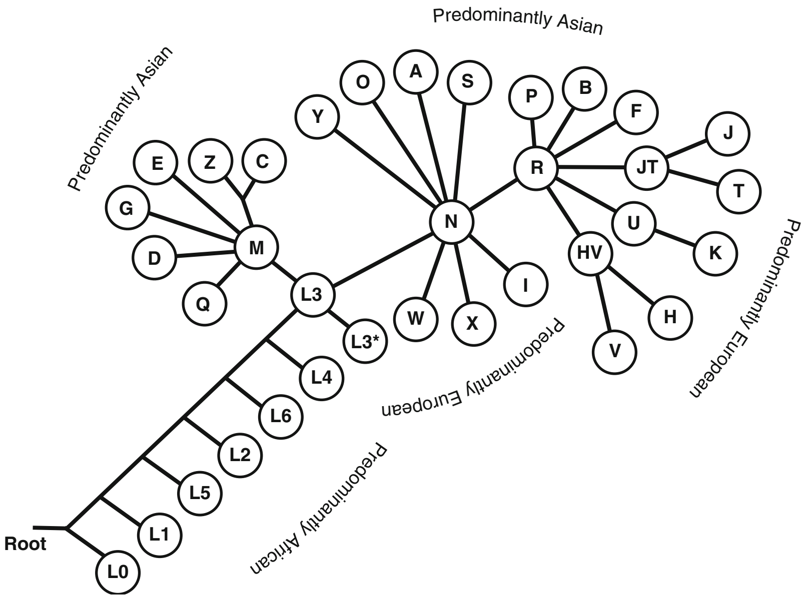

Fig. 3 Mitochondrial DNA haplogroup phylogeny with arbitrary branch lengths (Modified from Ruiz-Pesini et al. 2007 and Behar et al. 2012)

Various criticisms of using mtDNA sequence data that have been put forth include the possibility of nonmaternal inheritance, selection skewing inferences of geographic structure and rates of evolution, and the presence of recombination. To date, no firm evidence of paternal inheritance has been demonstrated in humans (Bandelt et al. 2005). Furthermore, a mechanism that destroys sperm mtDNA has been discovered, making paternal inheritance even more unlikely (Nishimura et al. 2006). Claims for selection acting strongly upon some human mtDNA lineages, especially related to humans' entry into colder climates, have been put forth (Mishmar et al. 2003; Ruiz-Pesini et al. 2004). Others interpret the evidence for selection as mainly for purifying selection with only a restricted amount of positive selection in a small portion of the mtDNA genome (Elson et al. 2004). Eyre-Walker and Smith (1999) suggested that mtDNA genomes undergo recombination making inferences about their evolutionary history much less straightforward. The suggestion that mtDNA undergoes recombination has been amply countered by further analyses (Macaulay et al. 1999).

All in all, mtDNA analyses provide a very powerful tool for inferring the evolutionary history of humans and provide a remarkably consistent story as additional data and techniques are brought to bear. Mitochondria, however, only yield a maternal history of the organisms under study. To better understand the overall evolutionary history of any group, both male-specific and biparentally inherited loci are also needed.

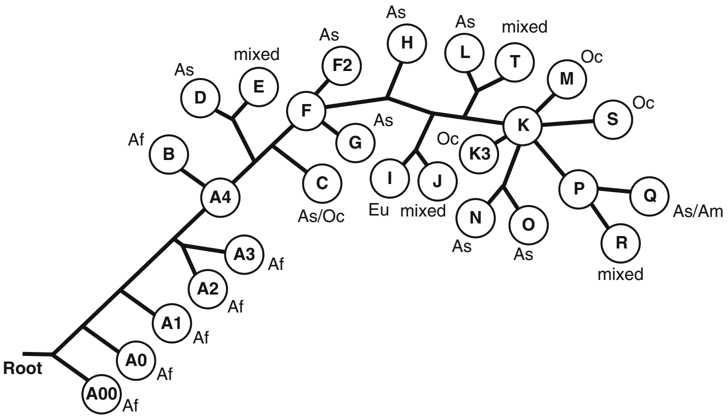

Fig. 4 T chromosome haplogroup phylogeny with arbitrary branch lengths. Labels outside terminal nodes describe the geographic origin of the majority of the individuals represented by the haplogroup (*Af* Africa, *Am* Americas, *As* Asia, *Eu* Europe, *Oc* Oceania) (Modified from van Oven et al. 2014)

The Y chromosome fulfills an analogous paternal role to maternally inherited mtDNA, as the majority of it does not recombine with regions of the X chromosome. This nonrecombining region (NRY) is also referred to as the male-specific portion (MSY) of the Y chromosome. While it was initially thought that little variation was present on the human Y chromosome, increasingly sophisticated molecular analytical techniques have allowed for the discovery of a wealth of variation and potential phylogenetically informative markers. Fortunately, unlike mtDNA, the naming of major lineages or haplogroups was regularized to unambiguously label the clades based upon their phylogenetic structure (The Y Chromosome Consortium 2002).

Early major research groups investigating human evolutionary history using Y chromosome markers inferred trees that have their deepest and next deepest roots within African populations (Underhill et al. 2000; Hammer et al. 2001; Jobling and Tyler-Smith 2003) (see Fig. 4). These studies also concurred in inferring a relatively recent African origin, around 100 Ka or younger with a more recent exodus into the rest of the Old World (Hammer et al. 1998; Underhill et al. 2000). This date is more recent than the mtDNA-derived estimate possibly because of the smaller effective population size of the human Y chromosome due to greater variation in reproductive success of males compared with females and the greater geographic structuring of Y chromosome variation. This apparent more recent common ancestry has been called into question by more recent studies involving more markers and more individuals. Cruciani et al. (2011) sequenced ~240 kb to better resolve the deeper lineages. Their study doubled the number of African-specific lineages and estimated the most recent common ancestor (MRCA) at 142 Ka.

Another study of 9 mega-base pairs (Mb) from over 1,200 males which using a rate of 0.53×10^{-9} bp^{-1} $year^{-1}$ (which is close to the estimates from triad de novo rates) found a MRCA of ~200 Ka (Francalacci et al. 2013). Mendez et al. (2013) discovered a new Y chromosome lineage in an African American individual that is also found in extremely low frequency in some Central Africans that they name A00. They inferred a MRCA date of 338 Ka and suggested either fundamental reassessment of the models for Y chromosome origins or the possibility of archaic hominin introgression. Elhaik et al. (2014) strongly critiqued Mendez et al.'s (2013) analyses on several grounds and recalculate the MRCA to 208 Ka. An analysis of 69 complete Y chromosome sequences estimates the MRCA between 120 and 156 Ka, in line with mtDNA estimates (Poznik et al. 2013). All these Y chromosome studies concur in the African origin of modern diversity, with the larger analyses placing the timing of this origin within the range of the estimated MRCA for mtDNA depending upon which evolutionary rates and fossil calibration points were used.

Pre-Second-Generation sequencing era studies were remarkably consistent. A study of over 10,000 base pairs on a region of the X chromosome with low levels of recombination also is compatible with the mtDNA and Y chromosome results. Kaessmann et al. (1999) found an approximately 535 Ka most recent common ancestor for the alleles of this region. This is broadly consistent with the mtDNA and Y chromosome dates, given that the effective population size of the X chromosome is three times that of the other two loci, so coalescent estimates will be approximately three times as old as well. A 3,000 bp region of the β-globin locus on chromosome 11 yielded an estimate of 750 Ka, which is again broadly consistent with being four times older then mtDNA and Y chromosome dates (Harding et al. 1997).

Nuclear loci such as the compound haplotype composed of an STR locus and an *Alu* deletion polymorphism on chromosome 12 at the CD4 locus demonstrate a similar pattern to the mtDNA and Y chromosome patterns of variation (Tishkoff et al. 1996). An African origin for the variation at this locus is estimated in the same time frame as that inferred from mtDNA and Y chromosome data with dramatically reduced variation found outside of Africa. Phylogenetic trees derived from numerous microsatellite (STR) loci similarly find their roots within Africa with reduced variation outside of it, though divergence date estimates cannot be easily calculated from such data (Bowcock et al. 1994). A similar pattern is found with SNPs (Yu et al. 2002) and polymorphic *Alu* insertions (Batzer et al. 1996).

Altogether, the majority of analyses of relatively short molecular sequences and markers suggest a recent African origin for the diversity of modern human genomes (Jorde et al. 2000; Takahata et al. 2001; Excoffier 2002; Satta and Takahata 2002). However, interpretations that contradict a scenario of a recent African origin have been put forth (Harris and Hey 1999; Hawks and Wolpoff 2001; Templeton 2005). Harris and Hey (1999), for instance, interpret PDHA1 (an X chromosome locus) sequence diversity as yielding a 1.86 Ma common ancestor, which would fall outside of the range of estimates derived from the above loci. The PDHA1 analysis has been called into question, due to the probability that the locus is under selection which makes inferences as to coalescence dates difficult (Disotell 1999). Nested clade analyses (Templeton 2002, 2005) suggest more than one major exodus from

Africa, an early one, approximately 1.9 Ma, one around 600–700 Ka, and a final one around 100 Ka with evidence for range expansion, long-distance dispersal, and isolation by distance complicating the picture. These analyses have generated a healthy skepticism, especially over the efficacy and accuracy of nested clade analysis (Cann 2002; Knowles and Maddison 2002; Satta and Takahata 2002; Panchal and Beaumont 2010).

Another approach to understanding our evolutionary history comes from examining the particular patterns of molecular variation found throughout the world. Several studies using microsatellite or short tandem repeat (STR) markers have found patterns that are best explained by a series of serial founder effects emanating from Africa outward to other regions of the world. Both Prugnolle et al. (2005) and Ramachandran et al. (2005) find the amount of genetic variation measured in a variety of ways linearly decreases the further populations are from Africa.

Analyses of the several thousandfold increase in amount of human molecular data collected with the advent of microarray SNP typing and Second-Generation (2ndGen) sequencing have corroborated most of the above findings. The Recent African Origin (RAO) model with important caveats discussed in detail below best explains the patterns of human molecular diversity observed today.

Neanderthals, Denisovans, and Other Archaic Hominins

Another opportunity for biomolecules to shed light on hominin phylogeny involves the direct characterization of DNA from fossils. While the earliest analyses of ancient hominin DNA focused on mtDNA, 2ndGen technologies now allow entire genomes to be sequenced. The presence of hundreds to thousands of copies of the mtDNA genome in most cells makes it an ideal candidate for extraction from poor or degraded sources of tissue, such as teeth and bone, including fossils. Ancient DNA (aDNA) analyses are however fraught with difficulties (Cooper and Poinar 2000; Mulligan 2005). Ancient DNA, when present, even under ideal preservation conditions is likely to be damaged and fragmented. More importantly, it is almost certainly contaminated with modern DNA from the environment, excavators, curators, scientists who have handled the material, and molecular laboratory personnel. Extraordinary precautions and techniques need to be carried out to lower the probability of mistakenly accepting such modern contaminants as the sequences from the ancient material (Cooper and Poinar 2000; Mulligan 2005). Despite these difficulties, aDNA provides a unique and important window in the evolutionary history and processes.

By the end of 2007, partial mtDNA sequences from around 18 Neanderthal individuals have been gathered (Krings et al. 1997; Ovchinnikov et al. 2000; Schmitz et al. 2002; Serre et al. 2004; Beauval et al. 2005; Lalueza-Fox et al. 2005; Caramelli et al. 2006; Lalueza-Fox et al. 2006; Orlando et al. 2006; Krause et al. 2007). These sequences form a reciprocally monophyletic clade with the thousands of modern human mtDNA sequences analyzed to date and are estimated to have diverged from modern humans somewhere between 365 and

853 Ka, with an average between 550 and 600 Ka. Even with this preliminary sampling of multiple individuals from different time periods and geographic locations, it is unlikely that a Neanderthal sequence that falls within the modern mtDNA gene pool will be discovered (Krings et al. 2000). Wolpoff (1998) suggested that because the original Feldhofer Neanderthal sequence is more similar to some modern human sequences than some other modern sequences are to other moderns, their mtDNA gene pools overlapped. This however was a misleading analysis as a cladistic analysis of the same data clearly demonstrates a complete separation of Neanderthals and moderns into reciprocally monophyletic clades (Disotell 1999). This observation has been further strengthened by all additional Neanderthal sequences and molecular analyses.

These Neanderthal sequences do not cluster among modern European sequences, as might be expected if they gave rise to the Europeans or extensively interbred with the new migrants into Europe as would be predicted under the multiregional model. However, both Nordborg (1998) and Relethford (2001) point out that different amounts of crossbreeding between Neanderthals and early moderns could have still been possible with the Neanderthal mtDNA lineages having gone extinct due to normal stochastic processes over the last 30 Ka. The Neanderthal sequences do show geographic and temporal structure however. The oldest sequences and eastern-most Neanderthals cluster together to the exclusion of western European samples younger than 48 Ka. Fabre et al. (2009) and Dalén et al. (2012) suggest that the western population may have experienced a bottleneck and population replacement while the eastern populations were more stable through time.

To further test hypotheses of modern human origins, several researchers have attempted to recover and sequence early modern human aDNA. One of these attempts provides a good illustration of the numerous difficulties of aDNA analysis. Adcock et al. (2001) claimed to have recovered an mtDNA sequence from an early modern human fossil skeleton from Australia, known as Lake Mungo III, then thought to date to approximately 60 Ka [this specimen has since been redated to 40 Ka (Bowler et al. 2003)]. The sequence fell outside of the range of modern human mtDNA diversity and clustered with a sequence located on chromosome 11 of the modern human genome, a known mitochondrial pseudogene (numt). Their interpretation was that early modern humans reached Australia before the most recent African exodus that gave rise to the rest of the world's mtDNA diversity less than 100 Ka. This analysis seems deeply flawed for several reasons. First, the standard protocols suggested to avoid contamination with modern DNA (Cooper and Poinar 2000; Mulligan 2005) were not rigidly followed (Cooper et al. 2001). The sequence is most likely in fact a contaminating numt or has been damaged to yield spurious nucleotide substitutions (Cooper et al. 2001). Smith et al. (2003) point out that it is extremely unlikely for aDNA to have survived at the Lake Mungo site due to the environmental conditions present. Finally, reanalysis with additional Australian and African sequences yields a tree very different from that originally put forth (Cooper et al. 2001). Caramelli et al. (2003) attempted to sequence several early modern specimens from Paglicci Cave in Southern Italy. Their sequences fully fall within the range of modern human sequences. These sequences are therefore either modern contaminants, or early modern mtDNA sequences indeed fall within the range of all modern mtDNA present today.

Serre et al. (2004) therefore took a different approach to investigating early modern human and Neanderthal mitochondrial diversity. They realized that demonstrating the presence of early modern mtDNA at that time was nearly impossible, so they tested five early modern fossil samples along with four Neanderthal samples for the presence of Neanderthal-specific mtDNA motifs. Included among the early human samples were fossils from Vindija, Croatia, and Mladeč (Czech Republic) that have been claimed to be transitional between Neanderthals and early moderns (Wolpoff 1999). Their reasoning was that, if interbreeding occurred between the two groups, the presence of Neanderthal mtDNA in early modern individuals would be more likely since it would not have had a great amount of time to go extinct as Nordborg (1998) and Relethford (2001) potentially proposed for the absence of Neanderthal mtDNA today. Serre et al. (2004) were able to amplify all four Neanderthal samples with "Neanderthal-specific" primers. None of the early modern human fossils yielded amplification products, though they did for more generalized "hominoid-specific" primers, suggesting DNA was present. Furthermore, faunal samples from the same sites all yielded DNA products, suggesting that the conditions at the sites were adequate for the preservation of aDNA.

Currat and Excoffier (2004) carried out a simulation study to model the conditions necessary to detect Neanderthal introgression with mtDNA. They extensively modeled different scenarios of modern human expansion into Europe with competition and admixture with Neanderthals. They found the mtDNA data at the time was only compatible with a less than 0.1 % interbreeding rate that would mean fewer than 120 matings over a 12,000-year period of overlap. One of the most important components of their model demonstrated that at the leading edge of an expanding population where interbreeding is most likely acts like a wave carrying new mutations and introgressed alleles to higher and higher frequencies. This iterative founder effect phenomenon is often referred to as "surfing the wave."

With development of 2ndGen sequencing methods, the potential of retrieving archaic hominin nuclear DNA improved dramatically. The first such studies (Noonan et al. 2006; Green et al. 2006) sampled a 38 Ka specimen (Vi-80) from Vindija Cave, Croatia, whose mtDNA analysis suggested contained 98 % endogenous Neanderthal DNA and only 2 % modern human contamination. Noonan et al. (2006) directly cloned DNA from the specimen (without amplification) and generated 62 kb of Neanderthal DNA. The sequences had the particular patterns of damage usually found in ancient DNA and were thus of presumed Neanderthal origin. They estimated an average divergence time between their sequences and those of modern humans at 706 Ka with the population split at 370 Ka.

Divergence time estimates for different loci within the genome will almost always be older than the population split, because nearly all populations have some level of variation within them. One test for the populations' divergence date is to look at variants within each population. For instance, if modern humans and Neanderthals separated a long time ago, Neanderthals would only rarely have the derived version of a modern human variant because if the variant appeared only in the modern lineage, and not in the common ancestor of modern humans and Neanderthals, the derived modern variant would not be found in Neanderthals. On the other hand, if Neanderthals and modern humans split recently or were significantly admixed, then derived modern human variants should be common in the Neanderthal genome. With only three derived modern human variants in their Neanderthal sample, Noonan et al. (2006) concluded that little to no interbreeding had occurred.

Green et al. (2006) using the same sample as Noonan et al. (2006) generated more than a million bases of sequence using a standard 2ndGen technique involving bead-based amplification. They estimated a divergence time of 516 Ka and found 30 % of the SNPs were identical to human-derived alleles. From this, they concluded significant admixture occurred. However, Wall and Kim (2007) demonstrated that much of Green et al.'s (2006) sequence was modern human contamination most likely introduced in the commercial facility utilized for the final sequencing. Thus, as of 2007, there was little evidence of any Neanderthal admixture with modern humans (Hodgson and Disotell 2008).

Using 2ndGen sequencing techniques, Green et al. (2008) generated a complete mtDNA genome from a Neanderthal from Croatia (Vindija 33.16). Briggs et al. (2009) sequenced five additional complete mtDNA Neanderthal genomes including Feldhofer 1 and 2, Vindija 33.25, El Sidrón in Spain, Mezmaiskaya 1, and Mezmaiskaya 2 (only a partial mtDNA genome) using a 2ndGen approach that targeted mtDNA. The younger individuals (38–70 Ka) had only about a third of the variation found in modern humans today, while the oldest sample was most divergent. The Mezmaiskaya 2 individual, despite only being 42 Ka, clustered with the younger western Neanderthals. A complete mtDNA genome from a 30 Ka modern human sample from Kostenki, Russia, was also sequenced using these techniques (Krause et al. 2010a). It clusters inside modern human haplogroup U2, which is common in North Africa, western Asia, and Europe.

With over two-dozen Neanderthal individuals sampled as of 2009, there was no evidence of mtDNA gene flow with modern humans (Currat and Excoffier 2004; Serre et al. 2004; Hodgson and Disotell 2008). With no sign of Neanderthal mtDNA in the tens of thousands of modern humans sampled to date, it was suggested that Neanderthal–human hybrids would have been rare while male hybrids might be sterile (Mason and Short 2011). According to Haldane's rule, the heterogametic sex in interspecific hybrids will be absent, rare, or sterile (Short 1997).

Improvements to 2ndGen sequencing techniques and new ways of avoiding or at least identifying contamination allowed Green et al. (2010) to successful produce a complete draft Neanderthal genome to 1.3-fold coverage. They generated 5.3 gigabases (Gb) of sequence from three Croatian female Neanderthal samples, using two different techniques that reduced microbial background and enriched the endogenous DNA present in the bones. They were able to cover about 60 % of the Neanderthal genome with less that 1 % error (Green et al. 2010). Along with the complete genomes of five diverse humans and small amounts of sequence from El Sidón, Feldhofer Cave, and Mezmaiskaya Neanderthals, they estimate the population split between humans and Neanderthals at occurred 270–440 Ka. Since modern human mtDNA coalesces around 200 Ka, the Neanderthal–human population split falls within the range of coalescence for nuclear genes (four times that of mtDNA). Therefore, it is expected that many alleles should be shared between humans and Neanderthals.

Green et al. (2010) found an excess of shared alleles between Neanderthals and the genomes they sampled from a French, Han Chinese, and Papua New Guinean individual but not two Africans (San and Yoruba). This suggests that non-African populations share more ancestry than African populations with Neanderthals, indicating some level of admixture. Interestingly enough, the Chinese and Papuan individuals share as much ancestry with Neanderthals as the French individual. By examining the extended haplotypes (regions of the genome that are similar between two individuals), they noted longer haplotypes in Neanderthals and non-Africans than in Africans. This suggests that the admixture was recent, since these regions were not broken up by recombination.

Green et al. (2010) estimated between 1 % and 4 % of non-African modern human alleles introgressed from Neanderthals. Furthermore, this gene flow was within the last 100 Kyr. They proposed two alternate scenarios to explain this admixture. Since the Neanderthal–human split occurred within the time frame in which modern human nuclear DNA diversity developed, if there was ancient substructure, the African modern human population, some African populations could be more closely related to Neanderthals than to others. If such a population or populations also later gave rise to the modern humans that exited Africa, non-Africans and Neanderthals would share more alleles than Neanderthals and other Africans. Given that only two African individuals were sampled, this could not be ruled out. Eriksson and Manica (2012) note that any analyses of potential admixture need to take such substructure into account. Yang et al. (2012) carried out simulations and compared them to data from the Complete Genomics Diversity Panel (Drmanac et al. 2010) and concluded that ancient African substructure does not explain Green et al.'s (2010) finding. Eriksson and Manica (2014) however argue that Yang et al.'s (2012) simulations were inadequate and ancient population substructure cannot be ruled out.

Green et al.'s (2010) favored scenario is that admixture occurred shortly after the modern human exodus from Africa carrying Neanderthal alleles both into western Asian and Europe as well as eastern and southeast Asia. One estimate of the timing of this potential gene flow is between 37 and 80 Ka (Sankararaman et al. 2012). Hodgson et al. (2010) suggested an alternative hypothesis in which limited admixture occurred slightly earlier, when African fauna and early modern humans expanded into western Eurasia around 100 Ka before retreating back into Africa due to climatic shifts. Neanderthal alleles would then be present in low frequency in northeast Africa. Populations from there later migrated out of Africa, either through the Sinai, the Arabian Peninsula, or both, carrying these alleles with them into Eurasia several tens of thousands of years later. These alleles would have become more common due to the iterative founder effect, surfing the wave to higher and higher frequencies in Europe and Asia (Currat and Excoffier 2004, 2011).

Updating their admixture models based on mtDNA (Currat and Excoffier 2004) to whole genomes, Currat and Excoffier (2011) found that under a wide variety of demographic scenarios, very low levels of interbreeding would be necessary to yield 1–4 % admixture. They further speculate that there would have been some kind of avoidance of interspecific mating or lower fitness in hybrids. They estimate that during the entire time and range of overlap, as few a few hundred matings may have occurred. Depending upon when and where those events occurred, different populations and different individuals are likely to share different Neanderthal alleles (Wills 2011). Vernot and Akey (2014) and Sankararaman et al. (2014) infer that up to 20–30 % of the Neanderthal genome is spread out among modern humans, a few nonoverlapping percent at a time.

With the continuing improving methodologies to extract and manipulate ancient DNA and higher and higher throughput 2ndGen sequencing technologies, an entire mtDNA genome followed by a 1.9× coverage full genome was generated from a 50 Ka partial juvenile distal phalanx and a single molar from Denisova Cave in the Altai Mountains of southern Siberia (Krause et al. 2010b; Reich et al. 2010). Using new techniques and remaining fragments of the phalange and some of the original extracted material, Meyer et al. (2012) generated a much higher coverage (31×) Denisovan genome which covers 99 % of the "mappable" genome. Despite being only 100 km from known Neanderthal sites, the Denisovan mtDNA genome is equally distantly related to both Neanderthals and modern humans, diverging around 1 Ma (Krause et al. 2010b). This date is too late to belong to *Homo erectus* and too early for the common ancestor of modern humans and Neanderthals. The Denisovan nuclear DNA on the other hand clusters with Neanderthals with an average divergence around 640 Ka.

The discrepancy between the mtDNA and nuclear divergence dates between Denisovans and Neanderthals could have two possible explanations. The Denisovans may have hybridized with an as yet unknown archaic hominin that migrated out of Africa after *Homo erectus* but before the common ancestor of Neanderthals and modern humans. Or, if the population that gave rise to Neanderthals and humans was quite variable and included the Denisovan haplotype, that haplotype may have gone extinct in both the modern human and Neanderthal lineages. This is known as incomplete lineage sorting. To date, neither of these hypotheses can be ruled out.

As interesting as the discovery of potential admixture between Neanderthals and Eurasians is the finding that up to 4.8 % Denisovan alleles are found in Melanesians (Reich et al. 2010). Along with 2.6 % Neanderthal ancestry, Melanesians may have up to 7.4 % of their genome composed of alleles found in archaic hominins. Denisovan alleles are also found in aboriginal Australians, near Oceanic, Polynesian, Fijian, and east Indonesian, but not south Asian or east Asian populations (Reich et al. 2011). Denisovans were also not very diverse, with only about 20 % of modern African and ~30 % of the variation found in Eurasians. There is also a reduced amount of admixed X chromosome alleles potentially suggesting it was mostly male-mediated gene flow. Unfortunately, all archaic genomes generated to date come from females, so we do not know what archaic Y chromosomes look like.

A toe phalanx discovered in 2010 in Denisova Cave has yielded an extremely high-quality (52× coverage) genome of a female Neanderthal (Prüfer et al. 2013b). With two high-quality archaic genomes now available, it was possible to estimate that the common ancestor of Denisovans and Neanderthals split from the modern human lineage between 553 and 589 Ka, while the two archaic lineages split approximately 381 Ka. The Altai Neanderthal was relatively inbred and probably derived from a population that went through a severe bottleneck. The higher-quality genomic data also reduce the amount of Neanderthal DNA thought to have introgressed into Eurasians to 1.5–2.1 %. Given that the branch length of the genome derived from the toe is shorter than the one derived from the finger, it is thought to be from slightly older sediments.

Further complicating the picture of admixture among the various hominins of the Middle Pleistocene is the observation that the mtDNA genome sequenced from a specimen from Sima de los Huesos in Spain is related to Denisovan mtDNA (Meyer et al. 2014). The Sima de los Huesos and Denisovan mtDNA genomes diverged around 700 Ka. The femur from which it was derived is classified as *Homo heidelbergensis* and is from sediments dated to over 300 Ka. Estimating the number of missing substitutions in the mtDNA genome, that is, those that would have occurred since the individual died, yields an expected age of 400 Kyr. Meyer et al. (2014) suggest that the most plausible evolutionary scenario is that the Sima de los Huesos hominins are broadly ancestral to both Denisovans and Neanderthals, which somehow maintained two deeply divergent mtDNA lineages.

Multiple scenarios are thus available to explain the complex patterns of relationships among the various Middle Pleistocene hominins and modern humans. The amounts, directions, and timings of introgression events are under healthy debate. There is still the possibility that what we are calling introgression may be the result of ancient population substructure (Eriksson and Manica 2014). Even the number of lineages involved is debatable. Does the Denisovan mtDNA haplotype represent another potential lineage? Hammer et al. (2011) infer approximately 2 % admixture from an unknown archaic population into some Africans population based on modern diversity in Africa. Similarly, based on whole-genome analyses, Lachance et al. (2012) infer introgression, from an unknown archaic population or populations, into Pygmy and click-speaking Hadza and Sandawe populations. Will east Asian fossils yield more surprises if or when molecular data is generated from them? Will the Flores Island specimens yield DNA with new and improved techniques, despite poor preservation?

Conclusions

Biomolecules have many advantages over morphological characters for phylogenetic analyses. The sheer volume of data potentially available is staggering. More importantly, nontrivial hypotheses regarding homology are generally more robust than those inferred for morphological characters and systems. The independence of characters and traits is more easily achieved at the molecular level, allowing multiple independent phylogenetic hypotheses to be generated and examined for concordance. On the other hand, all molecular phylogenies are necessarily gene trees, which can have different histories from the species or populations in which they reside. With whole-genome sequencing now available, including for a limited number of fossil taxa, the complexities of evolution are more readily apparent. Homoplasy and selection are more easily detectable at the molecular level. With high-quality ancient genomes, molecularly derived estimates of the ages of fossils are now possible. Fossils, on the other hand, can test hypotheses that have been put forth and suggest novel combinations of traits that we are not clever enough to have thought possible. A combination of approaches and techniques will provide us with the best insights into our evolutionary history.

Cross-References

▶ Analyzing Hominin Phylogeny: Cladistic Approach
▶ Ancient DNA
▶ Chronometric Methods in Paleoanthropology
▶ Historical Overview of Paleoanthropological Research
▶ Molecular Evidence on Primate Origins and Evolution
▶ Neanderthals and Their Contemporaries
▶ Origin of Modern Humans
▶ The Miocene Hominoids and the Earliest Putative Hominids

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The Miocene Hominoids and the Earliest Putative Hominids

Brigitte Senut

Contents

Abstract

For many years molecular studies suggested that the hominid family emerged during the Pliocene. But today we have good evidence of hominids in African Upper Miocene strata. Reconstructing our earliest history is a difficult task as the Miocene data is scanty and fragmentary. Furthermore, the tendency for

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B. Senut (✉)
Sorbonne Universités – CR2P – MNHN, CNRS, UPMC-Paris 6, Département Histoire de la Terre,
Muséum National d'Histoire Naturelle, Paris, France
e-mail: bsenut@mnhn.fr

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anthropologists to consider the modern chimpanzee as a good model for the last common ancestor of African apes and hominids has obscured our understanding of hominid evolution because the supposed distinctive apelike features are defined on the basis of a modern animal and not on those of Miocene hominoids. Taking into account detailed studies of Miocene apes and modern hominoids, it appears that bipedalism is probably the most reliable feature for defining hominids. Of the new hominoid taxa discovered in the Upper Miocene, only *Orrorin tugenensis* exhibits clear evidence of adaptation to bipedalism. Bipedalism in *Sahelanthropus tchadensis* and *Ardipithecus kadabba* still needs to be demonstrated. A long-lasting idea in hominoid evolution was that hominids emerged in dry, savanna-like environments; but the data obtained from the Upper Miocene levels in Baringo (Kenya) demonstrate that the environment of the earliest hominids was more forested and humid than expected. Finally, recent discoveries of modern-looking apes made in 12.5 Ma strata at Ngorora (Kenya), 10.5 Ma strata at Nakali (Kenya), 10 Ma strata at Chorora (Ethiopia), 11–5.5 Ma strata in Niger, and 6 Ma deposits at Kapsomin and Cheboit indicate that the dichotomy between African apes and humans could be much older than generally thought. Alternatively, one or more of these hominoids could represent early stages in the lineages of modern African apes.

Introduction

Identifying the earliest hominids remains a difficult task because the definition of the family varies widely from author to author. For some authors, the term hominid should be restricted to humans and their bipedal predecessors, whereas for others, it should include all extant and fossil great apes and humans; at its most extreme definition, all African apes should be included in the genus *Homo* (Czelusniak and Goodman 1998), or, in a slightly less extreme view, only chimpanzees and bonobos (with the exclusion of *Gorilla*) should be grouped with *Ardipithecus*, *Australopithecus*, and humans in this genus (Wildman et al. 2003). In the latter scenarios, the search for the oldest hominid leads to a strange situation where the quest becomes that of identifying the earliest ape rather than the earliest humans! This is definitely not what the theme of research on the origins of humans is today. The only consensus today among scientists (molecularists and anatomists) in ape evolution is that *Pongo*, *Pan*, and *Gorilla* do not belong to the same taxonomic group, a view that was widely accepted in the last century; the family Pongidae is now restricted to *Pongo* (Greenfield 1979). *Homo* is closely related to African apes and may be closer to *Pan* than to *Gorilla*. The modern tendency to use the term "hominines" is also misleading, as usage of the term varies: for some scientists, it gathers *Pan* and *Homo* and their ancestors, and for others, it is restricted to *Homo* and its forerunners. This is confusing, as the authors generally do not specify in which sense they use the term. This is why it is more appropriate to restrict the term Hominidae to humans and their fossil forerunners.

Whatever systematic scheme is considered, the focus is on understanding the ancestors of humans after their split from African apes. To understand the earliest hominids and ape cousins, we need to apply a geohistorical approach. The role of Asia as well as Africa in the history of our origins cannot be dismissed out of hand. However, today it seems clear from available field data that the development of the human lineage occurred in Africa.

Finally, we must consider the fact that, for the last 40 years, the history of research into the dichotomy between apes and humans has been dominated by the conflicting results obtained by paleontologists on the one hand and molecularists on the other. The debate has focused on two major aspects: chronology and the search for the closest relative. There was a heated debate in the 1970s concerning the molecular clock and its implications for hominid evolution versus paleontological evidence and geological time. But discrepancies in the time scales produced by various neontological studies have never been thoroughly debated, as pointed out by Arnason and coauthors in 2001. We have known for almost two centuries that the African apes are our closest relatives; but the research published in the last three decades has attempted to focus on the question in greater detail, and this has led to another major issue: Is the common chimpanzee the closest relative of humans? Or is it the bonobo? Or is it the group of African apes as a whole? At this point it has become widely accepted, almost without debate, that the closest human relative is the chimpanzee, frequently claimed to share 98 % or more of its genetic material with humans (or even 99.4 % for some authors such as Wildman et al. (2003)). General acceptance of these figures has occurred despite the fact that the problem is not yet definitively solved (Marks 2002).

It is within this complex framework that research on our oldest ancestors has taken place during the past three decades. In addition, preconceived ideas about our earliest relatives make it even more difficult to have a dispassionate discussion. A statement such as "the common ancestor of human and chimpanzees was probably chimpanzee-like, a knuckle-walker with small thin-enamelled teeth" (Pilbeam 1996) takes us back 200 years, being no different from the quest for the missing link. This widespread preconception is probably one of the reasons why many anthropologists have used modern chimpanzees as the basic comparative material when researching hominid origins and why the reconstructed late common ancestor was depicted as a bipedal chimpanzee.

This brings us to another aspect of the problem of defining the earliest hominid. Most anthropologists consider that apelike (i.e. chimpanzee-like) features are primitive and that humanlike ones are derived. However, chimpanzees are not primitive; they are in fact highly derived in their locomotor and dietary adaptations, and the use of their features as ancestral traits is a major error. Humans are also derived in their locomotion, but in a different way from chimpanzees. It is therefore not possible to define the polarity of these traits on the sole basis of some modern relict species; the Miocene apes were highly diverse, and this diversity has to be considered when reconstructing phylogenies. The neontological approach, which has been in favor in some scientific circles, turns out to be a total failure when dealing with the definition of the earliest hominids. This approach leads to a search for magic traits, such as flat face, small canines, and thick-enameled teeth, which are considered almost universally to be hominid features: for when only modern chimpanzees and humans are compared, these features seem to be obvious and clear. However, it is necessary to understand their meaning and their emergence before using them as a reference. When Miocene hominoids are included in the study, these same features are found to occur in many of them, suggesting that a flat face, small canines, and thick-enameled cheek teeth are plesiomorphic and that the elongated face of chimpanzees and their large canines and thin-enameled cheek teeth are apomorphies of the chimpanzee clade, rather than plesiomorphies of hominoids. Exclusion of the Miocene fossils from the comparisons of modern apes and humans erases the diversity of the past which is the raw material for understanding our evolution.

African or Eurasian Origins?

Determining a place for the origin of hominids (sensu stricto) has been widely debated for several decades, and some authors have suggested that Eurasia would be a better candidate than Africa (Begun 1992, 2002; Begun et al. 2012). However, these suggestions are based on biased data concerning Africa. The fact that hominoids were highly diverse in Eurasia between 13 and 8.5 million years does not mean that Africa was devoid of them in the Middle and Late Miocene. They have been recorded in Kenya, Ethiopia, Namibia, Chad, and Niger (Figs. 1 and 2). There is thus no reason to favor Eurasia in the origins of modern African hominoids

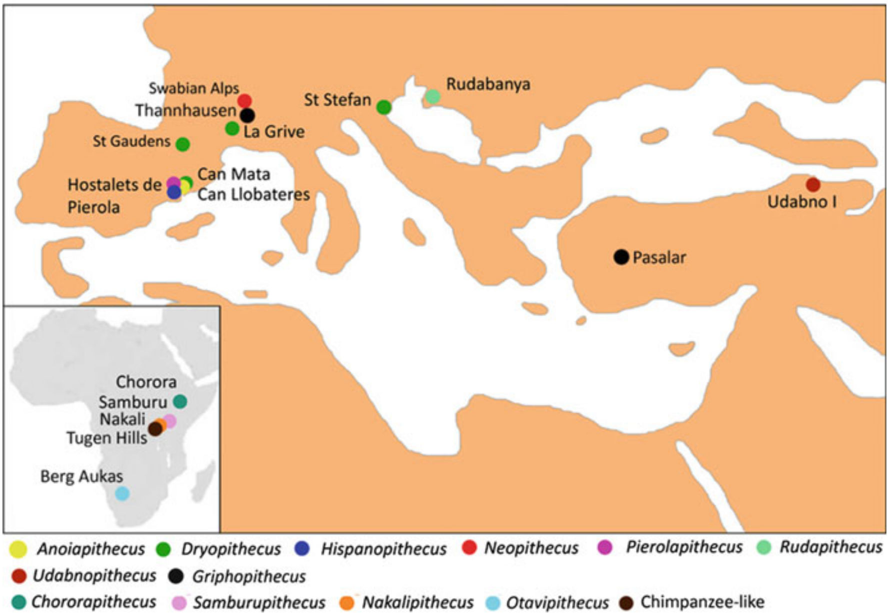

Fig. 1 Distribution of Late Middle Miocene and early Upper Miocene hominoids (Map modified from Begun et al. 2012)

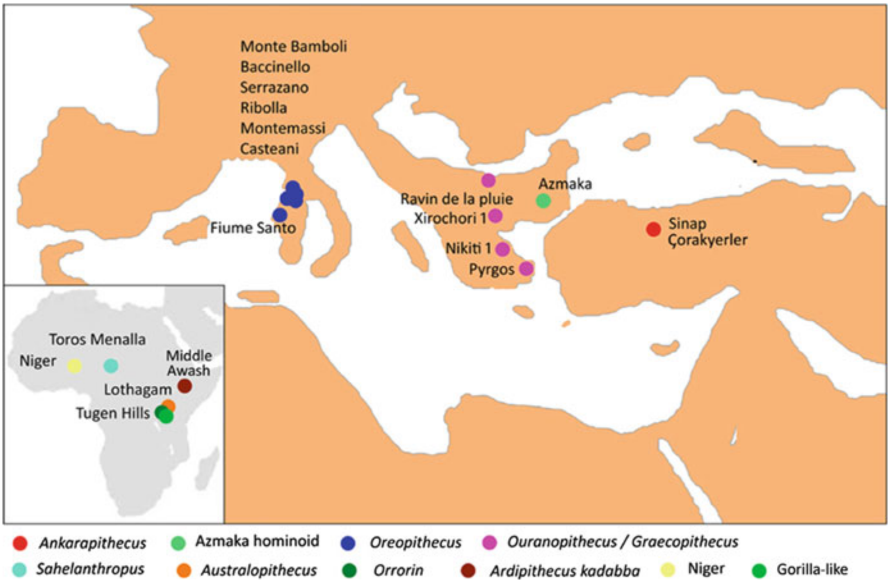

Fig. 2 Distribution of Upper Miocene hominoids (Modified from Begun et al. 2012)

(hominids included), and the "Back to Africa" hypothesis does not appear tenable today (Senut 2011a). However, does this necessarily mean that an African origin is the correct scenario? When climatic data are taken into account, it is possible to suggest yet another scenario. Nonhuman hominoids are basically tropical animals, and all through their 25 My-long history, they inhabited tropical areas, as indicated by floral and faunal data. Taking that into consideration, the most logical idea is to consider that their ancestors inhabited tropical regions and that faunal interchanges (including hominoids) occurred between Africa and Southern Eurasia throughout the Middle and Upper Miocene (the Tethys did not act as a permanent uncrossable barrier) (Senut 2011, and references therein). In the Early Miocene most of Africa was tropical, and the distribution of hominoids was Pan-African. When the Antarctic ice cap expanded to cover the entire continent at about 17 Ma, the Earth's climatic belts shifted northward such that midlatitude Eurasia became subtropical, allowing hominoids to disperse into vast areas of the Old World from Spain in the West to China in the East (Fig. 3). For several million years, faunal interchanges were possible between Eurasia and Africa, and hominoids could probably move freely between the continents in relation with paleogeography and the position of the tropical zones. This is why a precise geographic origin for African apes and humans cannot be proposed, although the paleoenvironment and paleoclimatic zone can be predicted with confidence (Fig. 4). However, for the moment the earliest modern-looking African apes and hominids are found only in Africa.

Still, the date of divergence between the different hominoids is not clear. Most biologists favor a young date for the split between humans and chimpanzees

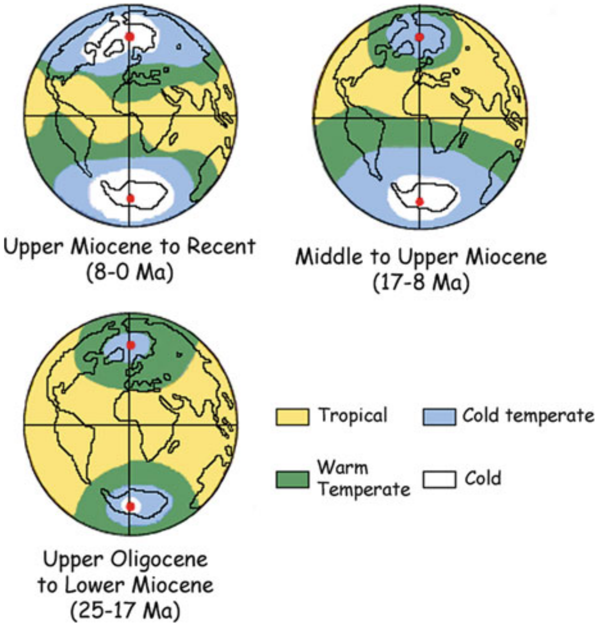

Fig. 3 Latitudinal shifts of the climatic belts during the Neogene. Being tropical mammals, hominoids followed these changes (From Senut 2011a)

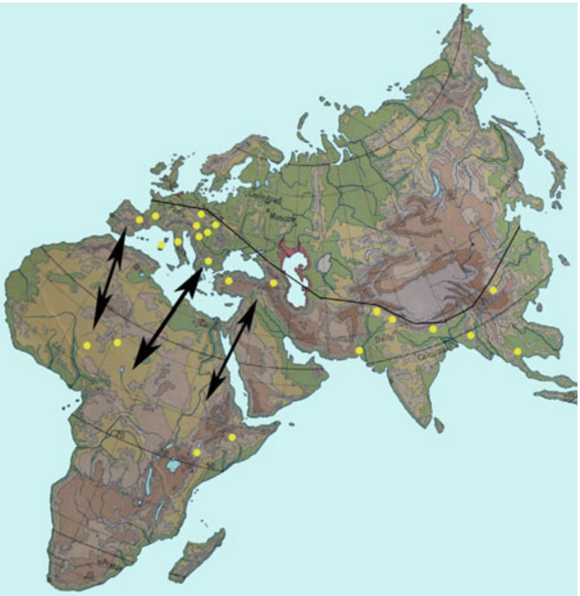

Fig. 4 Distribution of hominoids during the Upper Miocene. Even though a precise geographic origin for African apes and humans cannot be proposed, the extension of the tropical area reflects the zone of possible dispersals between Europe and Africa

(around 6 million years); but the calibration of the so-called molecular clock is not independent, as it needs an expected divergence date for some mammal lineages. However, some geneticists had already suggested other split times for hominoids (Arnason et al. 2001). In contrast, paleontologists usually tended to support older dates of 8–10 million years, or even older, for the split. But new dates of divergence, based on comparative generation time estimates in great apes compared with humans, and then using estimated mutation rates in humans provide a new look at the issue which accords better with the dates based on fossils (Langergraber et al. 2012). The split between chimpanzees and humans is now estimated to be 7–13 Ma, and the divergence between *Gorilla* and the lineage leading to the ancestor of chimpanzees and humans is between 8 and 19 Ma. Modern hominoid lineages are known from the Upper Miocene, indicating that their history was probably more ancient than previously thought.

The Rise and Fall of the *Ramapithecus-Kenyapithecus* Group

During the 1960s and 1970s, it was widely claimed that *Kenyapithecus* (sometimes considered to be an African relative of the Asian *Ramapithecus*) was a hominid, aged ca 15 Ma. This idea (Simons 1961; Simons and Pilbeam 1965; Leakey 1961/1962; Andrews 1971) was questioned by some morphologists (Genet-Varcin 1969; Greenfield 1978). The divergence between apes and humans was thus considered by these authors to be very ancient (about 16 Ma or even close to 20 Ma). But in the 1970s, the development of molecular biology and the application of the molecular clock led to the notion that the dichotomy was considerably more recent, and ages of divergences for the African great apes and hominids of about 2–4 Ma were proposed (Wilson and Sarich 1969). It was in this context, 30 years ago, that "Lucy" and the Afar australopithecines were discovered in more than 3 Myr-old deposits (Johanson and Taieb 1976). Considered at the time to be the earliest hominid, these fossils were later named *Australopithecus afarensis* (Johanson et al. 1978). This major discovery was widely acclaimed: for the first time, we could examine a quasi-complete fossil skeleton from an early time; the earliest stages of bipedalism (a key feature in the definition of hominids) could be seen, and we could get information on body proportions of the earliest members of our family Hominidae. Not least, "Lucy" was considered by many to occur in the range of dates estimated by the famous molecular clock, which at the time suggested that the dichotomy between apes and humans took place about 4 million years ago (Wilson and Sarich 1969).

Subsequently it was demonstrated that the molecular clock was not reliable, as it did not run at a constant rate in mammals and in particular in primates (Britten 1986; Pickford 1987; Stanyon 1989). In numerous papers a large variety of dates was advanced for the dichotomy between apes and humans, depending on the calibration ages accepted in the particular study and the type of protein used: these dates ranged from 2.5 Ma up to 4 Ma. But the fossils always seemed to give an earlier date. The question of an early or a late divergence was addressed by Greenfield (1980): he had already proposed that *Sivapithecus* (= *Ramapithecus) brevirostris* and *Sivapithecus* (= *Kenyapithecus*) *africanus* were size variants of *Sivapithecus*, and he suggested a late divergence for the group of *Homo*, *Pan*, and *Gorilla* from the pongid stock. However, the age of this dichotomy that he published (10–5 million years) was greater than the one proposed by geneticists.

Following general acceptance of the molecular evidence that supported a divergence between chimpanzees and humans around 4 Ma, the matter of chronology was thus thought to be solved and neither *Ramapithecus* nor *Kenyapithecus* was subsequently considered by many authors to be hominid. By the end of the 1970s, the *Kenyapithecus* material had been restudied, especially in the light of sexual dimorphism in modern and fossil apes (Greenfield 1978, 1979; Pickford 1986; Pickford and Chiarelli 1986). It transpired that the group of Ramapithecines-Kenyapithecines did not belong to Hominidae, and as a result the Middle Miocene estimates for the dichotomy between apes and humans were abandoned. Eventually, a meeting organized at the Vatican in 1982 led to a consensus between paleontologists and molecularists: the divergence occurred at around 7 Ma.

However, despite the fact that several isolated fossils of putative early hominid ancestors were already known at that time, such as the Lothagam mandible thought to be close to 7 million years old (Patterson et al. 1970), the 6 million year-old Lukeino lower molar (Pickford 1975), and the 4 million year-old Kanapoi humerus (Patterson 1966; Patterson and Howell 1967), these materials were too fragmentary to be taken seriously by most paleoanthropologists, and there was a tendency to avoid them in the phylogenies. Then Coppens (1983) reconsidered all the hominoids, some of which had been attributed to hominids. Taking into account environmental changes, chronology and geography, he formalized his "East Side Story." He suggested that around 7 Ma the ancestral population to African apes and humans was divided by the formation of the Great Rift Valley, which would have led a modification in the rainfall: which remained high in the West but was reduced in the East. The apes would have survived in the West in wooded and forested environments, while hominids became adapted to wooded grasslands and more open environments in the East. He later updated the theory and suggested an age of 10 Ma for the split between apes and hominids (Coppens 1986; Senut 2006b).

Until the end of the twentieth century, australopithecines were considered to be direct ancestors of humans, even though some scholars pointed out that more modern forms existed during the same period, implying that Plio-Pleistocene hominids were more diverse than expected, and that australopithecines might have been a side branch of human evolution (see Senut 1992 and Pickford 2012 for reviews). But by the end of the twentieth century, it was widely accepted that the earliest hominid ancestor was to be found in the early Pliocene.

Bipedalism and Its Impact on the Origins of Hominidae

Among living primates, facultative bipedalism is frequent; but even if most primates can sit with the back upright, stand on two feet, and walk bipedally for short distances, humans are the only ones that can move on two legs for long distances and for extended periods of time. This difference is reflected in the skeletal characters of extant humans, often defined in comparison with chimpanzees. While a suite of putatively bipedal features linked to femoral, pelvic, or sacral morphology appears to be soundly based, others are questionable. This is the case with the position of the foramen magnum. For the past 80 years, following Dart (1925), most scientists have considered that an anterior position of the foramen magnum indicates bipedality in hominids. Le Gros Clark (1950) used the anterior position of the occipital condyles to confirm the hominid nature of the australopithecines and proposed a "condylar position index," but he noticed that in modern humans this position varied between dolichocephalic and brachycephalic individuals. Later (Le Gros Clark 1972), the same author warned: "It has been assumed that the condylar-position index, by itself, is always correlated with the degree of postural erectness. The fallacy of this assumption is exposed by the fact that the index varies quite considerably even in modern *H. sapiens*." However, generic, specific, and/or populational studies remained limited before 1960, despite the fact that Schultz (1955) highlighted the variability of this feature. Since then it has been shown that an anterior position of the foramen is not linked exclusively with bipedalism, but could be related to the development of the brain (Biegert 1963). Several authors demonstrated that its position relative to the cranial foramina was variable (Dean and Wood 1981, 1982; Schaeffer 1999). It is difficult to discriminate individuals on these isolated features, as there is an overlap between apes and humans. Moreover, it appears that the foramen magnum is more anteriorly displaced in australopithecines than in humans, even though they were not better bipeds than we are. This feature is more complex than usually thought, and we must be cautious when using it.

Different forms of bipedalism have existed in the past. Of these, the most debated concerns *Oreopithecus bambolii*, discovered in the Late Miocene lignites of Tuscany (Hürzeler 1958; Schultz 1960; Straus 1963; Tardieu 1983; Sarmiento 1983; Senut 1989 and see review in Senut 2011b) and which was later demonstrated to be bipedal (Köhler and Moyà-Solà 1997; Rook et al. 1999). For the pedal features, these authors showed that this Miocene ape could move bipedally when on the ground but with a stabilization morphology that differed from those of humans and australopithecines. *Oreopithecus* lived in an island environment where the absence of large predators and limited trophic resources played an important role in the evolution of mammals (Köhler and Moyà-Solà 1997).

The most convincing bipedal evidence from the Upper Miocene remains *Orrorin* (Pickford et al. 2002; Galik et al. 2004; Richmond and Jungers 2008; Almecija et al. 2013) based on the femoral anatomy and morphometrics in different independent studies. Despite the fact that *Orrorin* is a biped, it is still moving in the trees as shown by other postcranial elements (Senut et al. 2001; Senut 2003). This ability is probably retained from older Miocene hominoids and is still present in australopithecines. This is also supported by the paleoenvironmental studies. Bipedalism and arboreality are major factors in our origins (Senut 2006b, 2012).

The Case of *Australopithecus afarensis* (= *antiquus*)

At one time or another, every single fossil older than *A. afarensis* from Afar in Ethiopia has been considered the earliest human ancestor; and this ancestor was almost always interpreted as being in the direct line leading to the genus *Homo* and thence to us. However, this approach ignored or underestimated the probable diversity of Pliocene hominids. In fact, in the late 1970s, several authors had already pointed out that there might be a taxonomic problem with the species *Australopithecus afarensis*: was it, as claimed, a single bipedal species? Did this species include two different taxa, one of which was a combination of a climber and a terrestrial biped and the other a more advanced species which was primarily a ground-dwelling biped? (See the review of *Australopithecus afarensis* locomotor adaptations in Stern (2000) and in Coppens and Senut (1991).) The difficulty derived mainly from the fact that before the 1970s scientists had built their phylogenetic trees almost exclusively on the basis of dental anatomy, whereas the incorporation of locomotor traits led to a modification of these phylogenies. The picture became more complex in subsequent years, with a crop of new species of australopithecines being created; several of these had specimens also included in other hypodigms. This was especially clear with *Praeanthropus africanus*, *Australopithecus afarensis*, and *Australopithecus anamensis*. The use of cladistic methods did not clear up the problem (Strait et al. 1997; Strait and Grine 1999, among others), as the *Praeanthropus* hypodigm of these authors does not include the same fossils as those proposed by Senut in 1996. The phylogenetic approach thus became more and more confused, various scholars using the same species names in different ways without defining them.

As discoveries became more and more numerous, several genera were resurrected or created: *Praeanthropus*, *Ardipithecus*, *Orrorin*, *Sahelanthropus*, and *Kenyanthropus*. New specimens of a Pliocene hominid, *Australopithecus prometheus*, were found in South Africa at Sterkfontein (Clarke 1995, 2013). But a major question remains unanswered: Is *Australopithecus afarensis* a direct ancestor or a side branch of our family?

The Upper Miocene Evidence

The majority of scenarios concerning the dichotomy of apes and humans, with the exception of the East Side Story of Coppens (1983), failed to take into account the environment. Coppens' hypothesis was ecogeographic in nature, the African Rift Valley constituting an ecological barrier between the apes in the West and early hominids in the East from about 7–8 Ma. But the most important elements of his hypothesis were chronological (the divergence took place between 10 and 7 Ma (Coppens 1986; Senut 2006b)) and ecological (climatic change engendering modifications in regional vegetation patterns, etc.); and, despite its name, the geographic element was subsidiary in the evolutionary scenario. As soon as we began to look for early and/or putative hominids in strata older than the Pliocene, we found them. In 2000, the discovery of early hominid remains (*Orrorin tugenensis*) in the Upper Miocene strata of Kenya, and subsequent finds in Middle to Upper Miocene sediments of the same country, shed new light on the question of our divergence from the African apes. The *Orrorin* discovery was subsequently followed by finds in Ethiopia (*Ardipithecus kadabba*) and then Chad (*Sahelanthropus tchadensis*). The debate mainly focused on the C/-P/3 complex and on adaptations to bipedalism. The status of the latter in the two last-named species is still a matter of debate, as the postcranial evidence is either poor or absent. But the main disagreement lies in the fact that in most studies comparisons were made basically with modern apes and later hominids and very little with Miocene apes. As pointed out above, structures or features supposed to be hominid apomorphies might well be retained from older Miocene apes; and some of the modern African ape features, usually considered to be primitive, might not be so.

Ardipithecus ramidus

In 1994 *Australopithecus ramidus* was published, and in 1995 it was attributed to the new genus *Ardipithecus*. This hominoid from Aramis localities 1–7 in the Middle Awash (Afar Depression in Ethiopia) (White et al. 1994, 1995) was pronounced to be the earliest-known hominid. All the specimens, except the humerus (which was found above the Daam-Aatu Basaltic Tuff), come from a level located between the Daam-Aatu Basaltic Tuff and the Gaala Vitric Tuff complex. The tuff complex, situated at the base of the section, has been dated at 4.39 ± 0.013 Myr, and an age between 4.2 and 4.5 Ma can be estimated for the fossil hominid (WoldeGabriel et al. 1994). At the time of the discovery, these fossils were among the few supposed hominids older than 4 Ma. Recently, a few more specimens have been described from the Early Pliocene at As Duma in the Gona Western Margin (Ethiopia). Their ages have been estimated at 4.51–4.32 Ma (Semaw et al. 2005). According to its discoverers, the new genus differed from *Australopithecus* by the reduced megadontia of the postcanine teeth; the greater width of the upper and lower incisors compared with postcanine teeth; a narrow and obliquely elongated lower dm1 with a large protoconid and a small, distally place metaconid without an anterior fovea; a small, low talonid with reduced cuspule development; absolutely and relatively thinner canine and molar enamel; and lower and upper P3s more strongly asymmetrical, with more dominant buccal cusps. With a canine that is not mesiodistally elongated, it is distinguishable from modern African apes. However, some of the cited features – including the thin enamel in the molars, asymmetrical upper and lower third molars, and the size relationships between the incisors and jugal teeth – place *Ardipithecus* closer to the chimpanzee than to any of the oldest hominids known (Pickford, 2012). The first deciduous molar shows resemblances to those of bonobos. But the morphology of the canine distances *Ardipithecus* from apes: it is more incisiform than in the latter group. Metric comparisons of the adult teeth were made with *Australopithecus afarensis* and underline the diminutive size of *Ardipithecus*. The upper canine/lower anterior premolar complex is typical of apes and was described as being "morphologically and functionally only slightly removed from the presumed ancestral ape condition" (White et al. 1994, p. 308) (though these authors also considered the modern ape morphology plesiomorphic). However, certain features taken as support for its hominid status occur in female apes, which have a reduced canine/premolar complex compared to those of males. Its postcranial bones reveal several apelike features, but the proximal humerus is more humanlike in the shallowness of the bicipital groove. However, this character occurs not only in hominids but also in other primates such as the cautious climber *Pongo* (Senut 1981). The fragment of occipital preserved would suggest that the foramen magnum is placed anteriorly relative to the carotid foramen, but for the reasons given above, we must be cautious with the interpretation of this feature. At the end of 1994, a skeleton (like a roadkill, according to the authors) was found in the Aramis strata. It was published in 2009 (White et al. 2009) and claimed to be the first representative biped of the human lineage. However, the traits proposed in evidence of bipedalism are not convincing. The reconstruction of the vertebral column is based on only two fragmentary vertebrae. And whereas the femur has been reconstructed to resemble a human one, only the shaft is preserved. This is very massive and robust and has nothing to do with the more gracile, elongated human femur. The humerus, which is not preserved, has been reconstructed like a human one. The bones of the forelimb are set wide apart, rather than close as in humans, and suggest massive forearm muscles as seen in modern African apes. The thumb is short, and its distal phalanx is not hominid-like in morphology. It is elongated and narrow, as in nonhuman hominoids, and lacks the hominid morphology seen in *Orrorin*, australopithecines, and *Homo*. The pelvis is strongly crushed, and the reconstruction appears more hominid-like, based on comparisons with *Australopithecus afarensis*. Despite the numerous papers on the functional anatomy, and given such weak evidence, it is difficult to accept bipedalism in *Ardipithecus ramidus*. The study suggests to me that *Ardipithecus* might be a fossil relative of the chimpanzee. Assuming that the features exhibited in modern chimpanzees were present in its forerunners has been a widespread theme among anthropologists, the bonobo long ago being considered a good model for the hominid ancestor (Zihlman 1984), although this was already criticized at that time (Senut 1988). The idea that the discovery of *Ardipithecus ramidus* led to the new idea that the chimpanzee is not a good model for the ancestor of hominids (Lovejoy et al. 2009) is thus actually not new. What is more, although the hypothesis appears to be right, it is based on wrong evidence.

Among other discoveries, Semaw et al. (2005) briefly described a proximal third of a pedal proximal phalanx from deposits of As Duma dated at 4.51–4.32 Ma. They wrote: “The transversely broad oval proximal facet is oriented dorsally, a character diagnostic of bipedality, and a trait also seen in Ardipithecus kadabba.” But Rose (1986) had already described the same feature in *Sivapithecus* from the Miocene of Pakistan, making it difficult to accept the proposed bipedalism in *A. ramidus*.

On the basis of the fauna and the botanical and sedimentological indications, the environment of *Ardipithecus ramidus* at Aramis is a forested one (WoldeGabriel et al. 1994). In the Gona sites, the faunal association, carbon isotopes, and sedimentology suggest a moderate rainfall woodland and woodland/grassland (Semaw et al. 2005).

Orrorin tugenensis

The discovery of *Orrorin* led to the elucidation of several aspects of early hominids (Senut et al. 2001). The specimens come from four sites: Cheboit, Kapsomin, Kapcheberek, and Aragai in the Lukeino Formation aged ca 6 Ma (6–5.8 Ma) (Bishop and Chapman 1970; Bishop and Pickford 1975; Chapman and Brook 1978; Kingston et al. 1994; Pickford and Senut 2001) (Fig. 5). The Lukeino Formation overlies the Kabarnet Trachyte dated by K/Ar, paleomagnetism, and biochronology

Fig. 5 Remains attributed to *Orrorin tugenensis* in 2000

at 6.1 Ma and is overlain by the Kaparaina Basalt the age of which is estimated to be 5.7 Ma (Sawada et al. 2002). In the section, Cheboit and Aragai are the oldest sites, followed by Kapsomin and then Kapcheberek which lies in the upper level of the formation. Up to now, 20 specimens of *Orrorin* have been found, consisting of the posterior part of a mandible in two pieces, a symphysis and several isolated teeth, as well as three femoral fragments, a partial humerus, a first phalanx, and a distal thumb phalanx. The genus is defined by its jugal teeth being smaller than those of australopithecines, an upper canine short with a shallow and narrow vertical mesial groove and a low apical height, a small triangular upper M/3, a lower p/4 with offset roots and oblique crown, small *Homo*-like squarish lower m/2 and m/3, thick enamel on the lower cheek teeth, a buccal notch well developed on the cheek teeth, no cingulum on the molars, a femur with a spherical head rotated anteriorly, the femoral neck elongated and oval in section, a medially salient lesser trochanter, a deep digital fossa, a humerus with a vertical brachioradialis crest, a curved proximal manual phalanx, and a dentition that is small relative to body size. *Orrorin* differs from *Australopithecus* in the morphology of the cheek teeth, which are smaller and less elongated mesiodistally. It differs from *Ardipithecus* by the greater thickness of enamel. It differs from both by the presence of a mesial groove on the upper canine. The upper and lower canines exhibit an apelike morphology, seen in female chimpanzees and Miocene apes; they are reduced in comparison with *Pan*. The apex of the upper canine is pointed and almost sectorial, and a poorly developed lingual wear facet is visible.

The femurs reveal that *Orrorin* was bipedal (Senut et al. 2001; Pickford et al. 2002; Galik et al. 2004). However, the other postcranial bones suggest that it could climb trees. The distal phalanx of the thumb exhibits features resembling hominids such as presence of a marked tuft (horseshoe shaped), deep depression for the *m. pollicis longus* with strongly asymmetrical edges, strongly asymmetrical basal tubercles, and a swelling at the base of the insertion of *m. pollicis longus* (Gommery and Senut 2006).

Some features of the hominid thumb are classically (but probably erroneously) associated with the manufacture of tools; these traits could be related to grasping abilities when climbing trees (Gommery and Senut 2006) (Fig. 6). At the time of its discovery, *Orrorin* was the first known bipedal hominid older than 5 Ma and indicated that the dichotomy between the African apes and the hominids had to be older than 6 million years and that the classic recent dates of divergences estimated by molecular biologists did not fit with the paleontological evidence. On the other hand, the locomotor and dental features suggest that *Orrorin* was different from *Australopithecus afarensis*. It was microdont with small postcanine teeth and a rather large body size, whereas *Australopithecus* was megadont with large postcanine teeth and small body size. Modern humans are microdont. Some morphometric studies have suggested that *Orrorin* is an ancestor of later australopithecines (Richmond and Jungers 2008). However, when checked in detail, it appears that their results could be interpreted either way, as *Orrorin* data fall close to australopithecines and *Homo*.

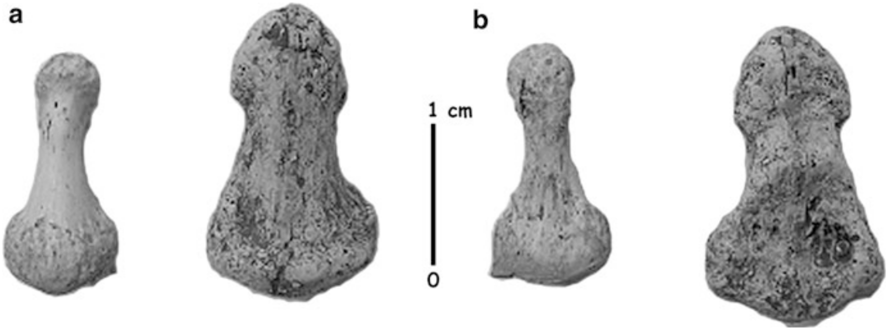

Fig. 6 Distal thumb phalanx of *Orrorin tugensis* (*right*) compared with an extant chimpanzee (*left*). (**a**) Dorsal view; (**b**) Palmar view (scale: 1 cm) (From Senut 2012)

Orrorin did not live in an open environment, but in a more forested one as suggested by faunal remains that include impalas, colobines, water chevrotains, arboreal civets, fruit bats and lorisids, and floral remains that contain large leaves with drip points (Pickford and Senut 2001; Senut and Pickford 2004; Senut 2006b), from which it is concluded that, in its early stages, bipedalism was not related to dry environments (Senut 2006b). Humid conditions persisted into the Lower Pliocene (Pickford et al. 2004). Stable isotope analyses of tooth enamel carbonate of large herbivores from the Lukeino and the Mabaget Formations are consistent with the first results (Roche et al. 2013) and refine them. They show that in the Early Pliocene and the latest Miocene, conditions were more humid than in the Upper Miocene. *Orrorin* inhabited a mixed C3–C4 environment comprised of thicket, woodland, and forest. Fossil leaves from the Lukeino Formation indicate the presence of woodland and dry evergreen forest, but some specimens suggest a more humid forest (Bamford et al. 2013).

Ardipithecus kadabba

Material discovered in Ethiopia (Haile-Selassie, 2001) from sediments aged between 5.2 and 5.7 Ma was identified as belonging to a subspecies of *Ardipithecus ramidus*, later raised to the specific rank *Ardipithecus kadabba* (Haile-Selassie et al. 2004). The material was collected at five different sites: Digiba Dora, Asa Koma, Alayla, Saitune Dora, and Amba East, from the Asa Koma Member of the Adu-Asa Formation. The first four are in the Asa Koma Member of the Adu-Asa Formation, and the deposits which have yielded the hominids are securely dated at 5.54–5.77 Myr by radiometric methods applied to underlying and overlying basalts. The Amba East material is slightly younger, being from the Kuseralee Member of the Satangole Formation dated 5.2–5.6 Ma (Renne et al. 1999). The morphology of the upper canine crown with a more rounded outline differs from *Orrorin*; but it also differs from *Ardipithecus ramidus* in the crest pattern of the same tooth as well as by a lower premolar that is more asymmetrical in outline and by the presence of a small anterior fovea. Moreover, the lingual cusps are more salient and sharp in the lower m/3 and the upper M3/ bears four cusps.

The species *Ardipithecus kadabba* differs from extant apes in its canines, which have a tendency to be incisiform as in *A. ramidus*, and by the presence of a clearly defined fovea on the lower p/3 which is isolated from the mesial marginal ridge by a fold-like buccal segment. However, some of the *Ardipithecus kadabba* dental specimens could belong to *Orrorin tugenensis*. It is difficult to know, as the material is not available for comparisons.

The postcranial morphology (Haile-Selassie 2001) indicates several similarities to African apes and selected specimens from the Hadar, but the shape of the ulnar olecranon differs from that of hominids. A proximal pedal phalanx resembles the ones from Hadar, and on the basis of the dorsal orientation of the proximal facet of the bone, it supposedly belonged to a biped. However, the curvature seen in the *Ardipithecus kadabba* phalanx might be linked with arboreal adaptations, as discussed by several authors (Susman et al. 1984; Stern and Susman 1983), and we must remain careful when assessing a locomotor complex on the basis of restricted material. *Ardipithecus kadabba* is associated with relatively wet and wooded environments as indicated by the fauna. However, the Amba East site seems to have been slightly drier (WoldeGabriel et al. 2001).

Sahelanthropus tchadensis

The discovery of *Sahelanthropus* in Chad was published in 2002 (Brunet et al. 2002). Announced as the earliest-known hominid, this status has been the subject of debate (Wolpoff et al. 2002, 2006; Wood 2002). It was found at Toros-Menalla (Chad) in deposits supposedly dated between 6 and 7 Ma, maybe closer to 7 Ma, by faunal comparison with the Lukeino Formation and Nawata Formation (Vignaud et al. 2002).

Recent Be/Al analyses performed on the levels hypothetically associated with the *Sahelanthropus* skull yielded a date between 7.2 and 6.8 Ma (Lebatard et al. 2008). However, some of the faunal remains found with the hominoid (discovered at the surface of the deposits), such as the Anthracotheriidae (Pickford 2008) and the fossil otters, could suggest the presence of two different biostratigraphic levels. In the latter case, data published on Dikika (Pliocene Australopithecine site in Ethiopia) (Geraads et al. 2011) based on results from Chad (Peigné et al. 2008) would suggest the presence of Pliocene fauna at Toros-Menalla. The age of the hominoid material remains uncertain.

The following diagnostic features of the species have been published: orthognathic face and weak subnasal prognathism; small ape-sized braincase; long and narrow basicranium; small canines; robust supraorbital torus; absence of supratoral sulcus; marked postorbital constriction; small, posteriorly located sagittal crest and large nuchal crest; wide interorbital pillar; low-crowned jugal teeth and enamel thickness between that of *Pan* and *Australopithecus*; and anterior position of the foramen magnum. It is considered to be different from all the living great apes because of the relatively small canines, the apical wear of the canines, and a probable non-honing C/-P/3 complex. The claimed hominid status is based on the small, apically worn canine and on the structure of the face. However, when these complexes are considered among all fossil and extant hominoids, it appears that they are more frequent than believed. The maxillofacial complex in extant apes varies according to sex, just as it does in Miocene hominoids (*Proconsul*, *Kenyapithecus*, *Ramapithecus*). It was this combination of features that originally led to *Ramapithecus* being proposed as a hominid, whereas it is today considered to be the female of *Sivapithecus*. Bipedalism in *Sahelanthropus* has been inferred from the position of the foramen magnum; but again, for the reasons expressed above, this feature can be misleading. The cranial base and nuchal area of *Sahelanthropus* (with its strongly developed nuchal crest and the flatness of the occipital) seem more apelike to some authors (Wolpoff et al. 2002, 2006), suggesting a quadrupedal posture and locomotion despite the reconstruction proposed by Zollikofer et al. (2005), which fails to contribute more evidence to the debate. The orientation of the plan of the foramen magnum falls within the range of variation of modern apes (Pickford 2005).

Whatever *Sahelanthropus* is, its status as a hominid is still debatable (Wood 2002), although it importantly fuels the debate on the origins of African apes and humans.

Sahelanthropus was found in perilacustrine sandstones, and the sedimentological context suggests a mosaic of environments between lake and desert, which have been compared with the modern Okavango delta. But the geological setting is different, as Lake Chad was much deeper in the Upper Miocene than the Okavango is today.

An Earlier Dichotomy?

During the past decade, several apelike fossils have been discovered in Africa that complete the data from the Samburu Hills (Ishida et al. 1984; Ishida and Pickford 1998). In the Baringo District of Kenya (Figs. 7 and 8), a lower molar in the 12.5 Ma Ngorora Formation and three fragmentary teeth from the Lukeino Formation are found in the same strata as *Orrorin tugenensis* (Pickford and Senut 2005); some isolated teeth at Chorora in Ethiopia are attributed to an ancestor of gorilla (Suwa et al. 2007). Also, a fragmentary mandible and isolated teeth come from Nakali (Kunimatsu et al. 2007), and a fragment of mandible of a proto-chimpanzee comes from Niger (Pickford et al. 2009). This new evidence sheds some crucial light on the dichotomy between African apes and humans.

Ngorora

In 1999, a lower molar was collected at Kabarsero, Ngorora Formation, Tugen Hills (Pickford and Senut 2005) 12.5 Ma (Bishop and Pickford 1975). This tooth, probably a lower m/2 (Pickford and Senut 2005), is close in morphology to *Dryopithecus* (Begun 2002) and chimpanzees and distant from similarly aged

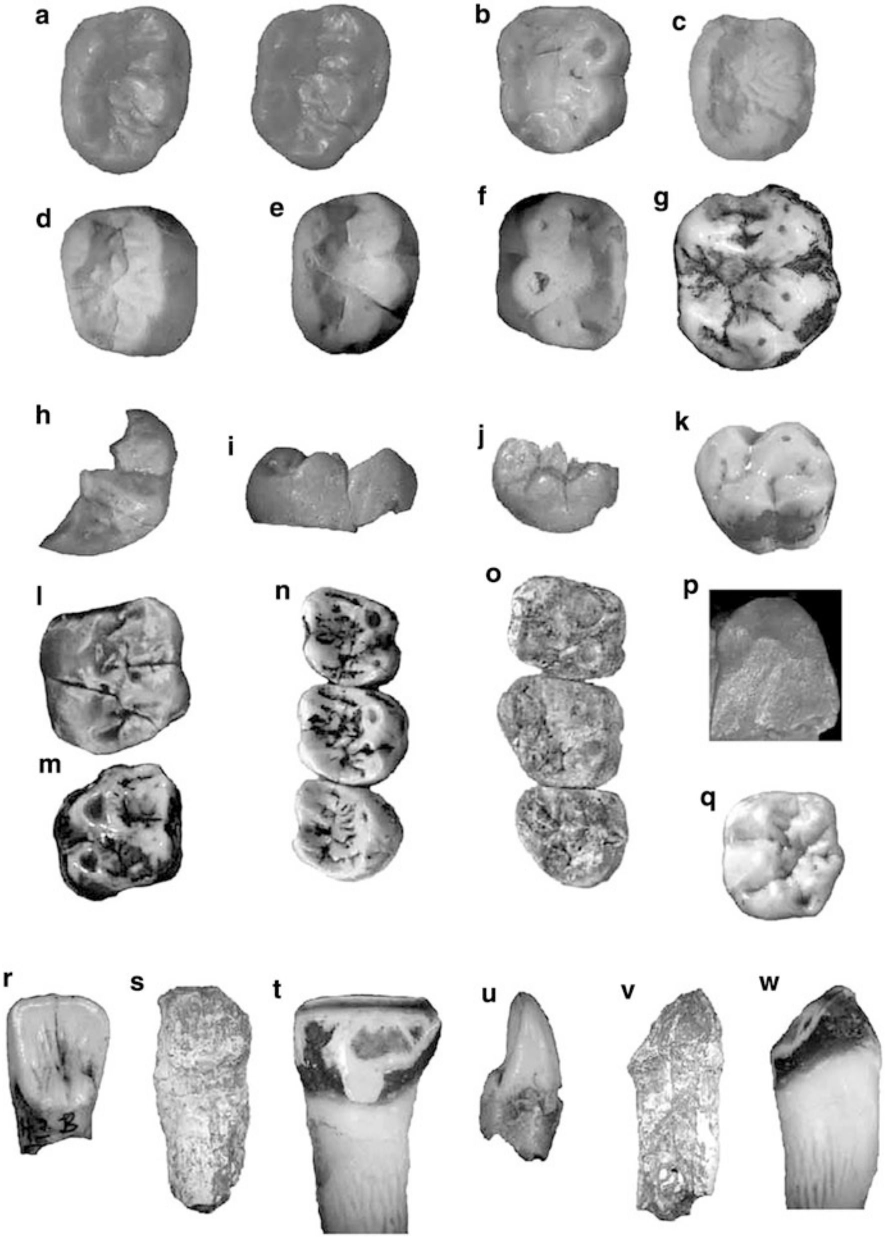

Fig. 7 (**a**) Bar 91'99, right lower molar, stereo occlusal view; (**b**) *Pan paniscus* right m/2, occlusal view; (**c**) *Pan troglodytes*, right m/2, occlusal view; (**d–f**) *Dryopithecus brancoi* lower molars from Europe, D = Trochtelfingen, E = Salmendingen, F = Ebingen; (**g**) *Gorilla gorilla* lower m/2, occlusal view; (**h–j**) Bar 1757'02, Kapsomin large ape, occlusal, lingual, and oblique views; (**k**) *Gorilla gorilla* lower m/2, oblique view; (**l**) *Australopithecus afarensis*, upper m/2, occlusal view; (**m**) *Gorilla gorilla* upper M2/, occlusal view; (**n**) *Pan troglodytes*, upper M1/–M/3 occlusal view;

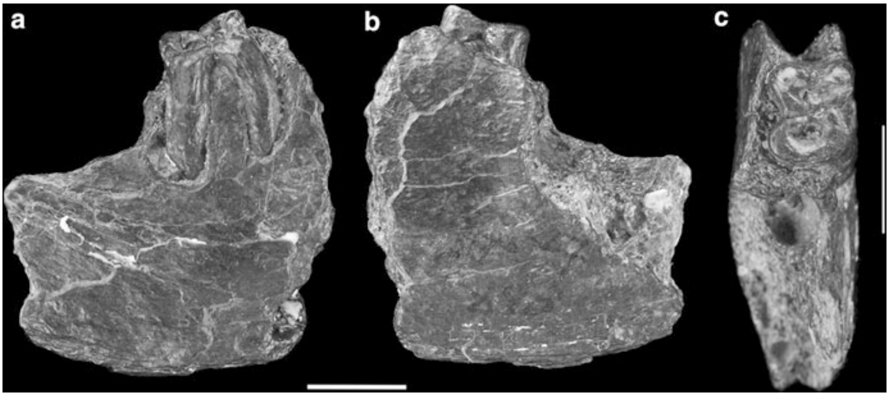

Fig. 8 Hominoid right mandibular fragment (1964-27-885) from Niger. (**a**) Buccal view; (**b**) Lingual view; (**c**) Occlusal view (scales: 1 cm)

Kenyapithecus and *Otavipithecus* (Conroy et al. 1992; Ward and Duren 2002). An upper molar had already been described from Ngorora (Bishop and Chapman 1970; Bishop and Pickford 1975; Leakey 1970), but it appears to be closer in morphology to *Kenyapithecus* (Ishida and Pickford 1998; Pickford and Ishida 1998; Senut 1998), and the thickness of the enamel and the more centralized cusps suggest that it belongs to a different hominoid from the lower molar. Two different kinds of hominoids would have coexisted at Kabarsero, a possibility which is also suggested in the lower (Napak) and middle (Moroto) Miocene sites of Uganda (Gommery et al. 1998, 2002).

If the derived characters of the Ngorora tooth are homologous to those of chimpanzees, then it would indicate that chimpanzees were already a separate lineage by the end of the Middle Miocene, a suggestion that accords with some interpretations of the molecular data (Arnason et al. 2001) and recent genetic studies (Langergraber et al. 2012). The resemblances between the Ngorora tooth and *Dryopithecus* indicate that the latter genus may have originated in Africa and migrated toward Europe about 12.5 Ma.

Chorora

Nine isolated teeth discovered in the Chorora area (site of Beticha) have been attributed to *Chororapithecus abyssinicus* (Suwa et al. 2007). They were found in

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Fig. 7 (continued) (**o**) *Orrorin tugenensis* upper molar row, occlusal view; (**p**) Bar 1757’02, detail of dentine-enamel junction at hypoconulid; (**q**) KNM LU 335, *Orrorin tugenensis*, left m/3, occlusal view; (**r**) *Praeanthropus africanus* cast of upper incisor from Laetoli, lingual view; (**s**) BAR 1001’01, Kapsomin large ape, I1/, lingual view; (**t**) *Gorilla gorilla* upper central incisor, lingual view; (**u**) *Praeanthropus africanus* cast of upper incisor from Laetoli, distal view; (**v**) Bar 1001’01, Kapsomin large ape, I1/, distal view; (**w**) *Gorilla gorilla* upper central incisor, distal view the upper part of the Chorora Formation dated at around 10.7–10.1 Ma. These teeth are close in size to, and resemble, those of *Gorilla gorilla*. They show clearly marked crests on the teeth, suggesting that they fed on fibrous plants that they sheared; but the cusps are less high and more peripheralized. The cingulum is weaker than in *Gorilla* and the thick-enameled molars are slightly larger. The faunal remains, rich in primates and poor in *Hipparion*, indicate that the environment of *Chororapithecus* was humid. Sedimentation suggests that *Chororapithecus* was living close to a lake shore and that there were alternating humid and more open spaces.

According to the authors, these teeth might represent a proto-*Gorilla*. If so, then, this find confirms the idea that the split between gorillas and chimpanzees and humans has to be at least 10 million years old.

Nakali

A few months after the discovery of the Ethiopian teeth, Kunimatsu and his team unearthed specimens belonging to another species of fossil hominoid from the Upper Miocene (9.88–9.80 Ma) at Nakali in Kenya: *Nakalipithecus nakayamai* (Kunimatsu et al. 2007). The reported material is composed of a posterior portion of a mandibular fragment and 11 isolated teeth. The teeth are close in size to females *Gorilla* or *Pongo*. The molars are thick-enameled, and their general morphology differs from other known hominoids in the canine and several premolar traits. It shares some similarities with the slightly younger *Ouranopithecus* from Greece but is more primitive. The authors suggest that it could be close to the last common ancestor to African apes and humans; but it could also belong to the lineage of the gorillas. Whatever it is, it evidences the fact that Africa was not devoid of large-bodied hominoids in the Upper Miocene.

Kapsomin

In 2002, half an upper molar of a large hominoid was found at Kapsomin, Lukeino Formation, aged 5.9 Ma (Pickford and Senut 2005). This tooth is larger than those of *Orrorin tugenensis* and the crown morphology is different. The trigon is wide, the distal fovea is broad, the main cusps are high and less inflated, and there is a deep buccal slit. Dentine penetration is also high. Most of these features occur in *Gorilla* and are different from *Pan*.

In 2000, an upper central incisor was found in the same strata as *Orrorin*. Originally assigned to *Orrorin tugenensis*, its morphology did not seem to fit with the early hominid. After a restudy of the specimen, it appears that it differs strongly from australopithecines and other hominids because of the lack of fossa on the lingual side of the tooth. Moreover, the crown is relatively low compared to root length, whereas in hominids the crown is higher with a scoop-shaped profile. In contrast, in *Gorilla* incisors, the lingual fossa is missing and the crown is wedge shaped as in the Kapsomin tooth.

In 2003, a lower molar was found at Cheboit, near the site of discovery of the first hominid tooth from the Lukeino Formation (Pickford 1975). The morphology of the tooth is compatible with the half upper molar from Kapsomin, and the specimens probably belong to the same taxon. As for Ngorora and the Ugandan sites, two different hominoids would have coexisted at Kapsomin in the same strata, 6 million years ago.

Niger

Discovered in 1964 in Niger, a right mandibular fragment with the roots of the lower M1 of a hominoid has been identified recently (Pickford et al. 2009). Comparisons with fossil and modern hominoids indicate similarities with *Pan troglodytes*. The faunal remains associated with the specimen suggest an Upper Miocene age between 11 and 5 million years. Furthermore, they suggest the presence of large river or a freshwater lake, indicating a more humid environment in the area than is the case today. This discovery is important, as it shows that hominoids were widespread in Africa in the Upper Miocene and it fills a gap in what is known of the distributions of African apes and their origins and sheds light on the dichotomy between humans and chimpanzees.

Conclusions

The debate about our earliest origins is probably not closed and is fueled by the poverty of fossils in the time period between 12 and 4 million years ago. This is why it is necessary to continue excavation and prospecting in different areas of Africa in order to fill the gaps and extend our knowledge of variation and diversity. As a matter of fact, recent surveys in Western Uganda led to the discovery of Upper Miocene and Pliocene faunas (including mammals) in an area supposed to be of Pleistocene age (Pickford et al. 2013). In Northern Namibia, new Upper Miocene and Pliocene deposits have been identified that have yielded mammals (Miller et al. 2010). One of the most troubling aspects of the research done to date on the origins of hominids relates to the comparative samples. Most scientists still focus on modern hominoids as a good reference for primitive morphologies. However, these animals are highly derived in their cranial and postcranial anatomy. As long as Miocene apes are not properly considered in these studies, we will remain trapped in the quest for a mythical missing link.

Of all the features used to define hominids, probably the least controversial is bipedalism. We know that in the past there have been several types of bipedalism, but there is definitely a basic one that is known in australopithecines, *Orrorin*, and *Homo*. In this group, adaptation to arboreality is variable: greater in some taxa, less in some others, and very little in *Homo*. There was probably a variety of early forms of hominids: the oldest widely accepted biped (supported by postcranial evidence) is *Orrorin*, and we await further data on *Ardipithecus* (arm, knee, and hip joints) and

Sahelanthropus to clarify their status (Fig. 3). What the evidence from the Upper Miocene tells us is that we cannot continue to support an origin of the earliest hominids in dry savanna-like conditions: in contrast, they inhabited humid to forested environments.

These early hominids cohabited with apes, and we are only just beginning to uncover the history of modern apes, of which we know only a small, emergent part of the iceberg: this is the challenge of the third millennium.

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Defining Hominidae
- ▶ Fossil Record of the Primates from the Paleocene to the Oligocene
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ Modeling the Past: The Primatological Approach
- ▶ Origin of Bipedal Locomotion
- ▶ Patterns of Diversification and Extinction
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Potential Hominoid Ancestors for Hominidae
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Earliest Putative *Homo* Fossils
- ▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments
- ▶ The Species and Diversity of Australopiths
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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The Species and Diversity of Australopiths

William H. Kimbel

Contents

Abstract

In this chapter, the historical, systematic, and anatomical evidence for the diversity of the species within the australopith grade is reviewed. Given a strict evolutionary species definition, nominal taxonomic diversity and species-lineage diversity do not necessarily map onto one another in the fossil record. Species lineages entail statements of ancestry and descent that depend on the consistency of phylogenetic and stratophenetic data. The requirements for identifying species lineages in the fossil record are severe and in the early hominin

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W.H. Kimbel (✉)
Institute of Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA
e-mail: wkimbel.iho@asu.edu

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record are rarely met, most often owing to small sample size, underrepresented character data, nonrepresentation of rare or short-lived taxa, poor chronological resolution, gaps in the time-stratigraphic framework, or some combination of these factors. Because hypotheses concerning the "bushiness" of the hominin phylogenetic tree depend on the identification of lineages, not phenetically based "paleospecies," confidence with respect to this issue is not justified for the majority of the hominin fossil record. There are two cases in which an approach to this question can be attempted. In one, the evidence is consistent with the evolution of *Australopithecus anamensis* into *A. afarensis* via anagenesis. The other, the evolution of *A. boisei*, most likely entailed a speciation event that gave rise to southern African clade (represented by *A. robustus*) subsequent to the appearance of *A. aethiopicus*. The late Pliocene time period in which the latter events transpired (ca. 2.8–2.3 Ma) is one of substantial morphological diversity, high nominal taxonomic diversity, and high probability of synchronicity among known fossil samples. With the exception of the close phylogenetic relationship of *A. africanus* to *A. sediba*, it is not possible to connect the later Pliocene australopith taxa (*A. aethiopicus*, *A. garhi*) to particular descendants due to defects in the database. Nevertheless, this time period probably documents a previously (and subsequently) unmatched degree of lineage proliferation compared to other parts of the human evolutionary record. The challenge to paleoanthropologists is to devote resources to improving this part of the fossil record and then to create testable phylogenetic and adaptive hypotheses to explain it.

Introduction

The australopiths constitute a taxonomically and adaptively diverse group of extinct hominins that are currently known to have inhabited the African continent between approximately 4.2 and 1.4 million years ago (Ma). The documented geographical distribution of this group includes present-day South Africa, Malawi, Tanzania, Kenya, Ethiopia, and Chad but certainly may have been wider. Evidence from pelvic, knee, ankle, and foot morphology and, where available, trace fossils (i.e., the Laetoli footprint trails) indicates that these hominins were terrestrial striding bipeds, more similar, if not identical, in their locomotion to living humans (and extinct representatives of the genus *Homo*) than to any other known primate, living or extinct. The australopiths were impressively more variable in their skull and dental morphology than in their postcranial form, though the latter is poorly documented for some of the species included in the group. Our understanding of their taxonomic and adaptive diversity therefore reflects an historically important preoccupation with anatomical distinctions above the neck, particularly in the dentition and the bony structures thought to be associated with the masticatory system.

Many more characters distinguish the australopith species from one another than link them together as a group. Apart from bipedality, shared australopith characteristics include:

1. An approximately ape-size brain (range ca. 375–550 cm^3)
2. Inferosuperiorly short, vertical midface with massive zygomaticomaxillary region and strong subnasal prognathism
3. Short, wide basicranium with anteriorly positioned foramen magnum
4. Absolutely small, nonhoning canines
5. Large (in relation to body size) premolars and molars capped by variably thick enamel
6. Transversely thick mandibular bodies and tall ascending rami

Although these traits may, in combination, identify the australopiths, they do not diagnose them as a "natural" (i.e., monophyletic) group, as none of the listed features is unique to the group (i.e., they are not autapomorphies; they are either symplesiomorphies-shared with the great ape outgroup to hominins, such as small brain size and strong subnasal prognathism, or synapomorphies-shared with one or more species in the closest sister taxon, *Homo*, such as bipedal locomotion, reduced canines, short cranial base, and, at least in comparison to some early species usually attributed to *Homo*, postcanine megadonty). As such, the australopiths most likely constitute a paraphyletic group, identified by its unique adaptive grade among the hominins (small-brained, small-canined, megadont bipeds). This idea is reflected in the entrenched tendency to use the genus *Australopithecus* as a "waste basket" taxon for any and all of the extinct hominin species whose skeletal and inferred behavioral characteristics fit this adaptive pattern, notwithstanding the likelihood that one or more monophyletic groups, such as the so-called "robust" australopith species (sometimes attributed to genus *Paranthropus*), are thus subsumed within it.

Historical Perspective on Australopith Diversity

The first described australopith species was *Australopithecus africanus* Dart 1925, identified on the basis of a fossil juvenile skull and brain endocast from the site of the Buxton Limeworks at Taung, Orange Free State (now Free State), South Africa. During the 1930s–1940s, no fewer than four additional species (in three genera) were identified based on adult craniodental fossils recovered from brecciated sediments within collapsed and eroded karstic structures then being mined for lime in South Africa (Sterkfontein 1936; Kromdraai 1938; Makapansgat 1947; Swartkrans 1948). The early taxonomy of the australopiths was authored by paleontologist Robert Broom (1950), who conducted the excavations at Sterkfontein, Kromdraai, and Swartkrans and perceived a different species at

Table 1 The evolution of australopith taxonomy during the 1950s

Site	Broom (1950)	Robinson (1954)
Taung	*Australopithecus africanus* Dart 1925	*Australopithecus africanus*
Sterkfontein	*Plesianthropus transvaalensis* (Broom 1936)[a]	*Australopithecus africanus*
Makapansgat	*Australopithecus prometheus* Dart 1948	*Australopithecus africanus*
Kromdraai	*Paranthropus robustus* Broom 1938	*Paranthropus robustus*
Swartkrans	*Paranthropus crassidens* Broom 1949	*Paranthropus robustus*

[a] Broom initially assigned the species *transvaalensis* to *Australopithecus*

each site (Table 1). Broom's protégé John Robinson subsequently collapsed this taxonomy to one species within each of two genera (Table 1) based on his scenario of a dichotomous partitioning of dietary resources by these early hominins (Robinson 1954). Robinson's simplified taxonomy and hypothesis of a morphologically specialized herbivore *Paranthropus* and a more generalized omnivore (and presumptively meat-eating and toolmaking) *Australopithecus* has had a profound effect on subsequent australopith systematics. It remains the leading explanatory paradigm for the evolution of these hominins to the present day.

Much of the early debate about the australopiths' role in human evolution had less to do with their adaptations or diversity than with their suitability as human ancestors. The skepticism that greeted Dart's claims of human ancestral status for *A. africanus* is well known, and despite the subsequent demonstration by Broom (1939; Broom and Schepers 1946), Gregory and Hellman (1939), Le Gros Clark (1947), and others of uniquely human characteristics in adult australopith teeth, jaws, and basicrania, it was not until the identification of humanlike bipedal adaptations – and the absence of apelike quadrupedal ones – in a distal femur (TM 1513) and capitate (TM 1526) from Sterkfontein and a talus (TM 1517) from Kromdraai that the most ardent skeptics capitulated (e.g., Keith 1947, though his recantation began earlier: from Robert Broom (Broom and Schepers 1946, p. 22)) we learn that "In a letter I have recently received dated 11th May 1944, Sir Arthur writes: 'No doubt the South African anthropoids are much more human than I had originally supposed, and I am prepared to swallow plantigrade adaptations in their limb bones'."

Although australopith fossils had lurked unidentified in east African faunal collections as early as 1935 (i.e., the BMNH M 18773 lower canine from Laetoli, Tanzania (White 1981)), it was not until the discovery of the Garusi (Laetoli) maxillary fragment in 1939 that attention was directed (albeit fleetingly) toward the East African Rift Valley as a source of early hominin fossils. The particularly apelike upper premolar and palate morphologies of the Garusi specimen were overshadowed by the powerful appeal of Robinson's adaptive scheme in which the fossil was cast as an east African representative of *A. africanus* (Robinson 1953a), and thus the Garusi maxilla receded into relative obscurity until the recognition of the craniodentally plesiomorphic *A. afarensis*, based on new mid-Pliocene Hadar (Ethiopia) and expanded Laetoli collections in the late 1970s (Johanson et al. 1978; see below).

Mary Leakey's 1958 discovery of the megadont *Zinjanthropus boisei* cranium OH 5 at Olduvai Gorge, Tanzania, together with discoveries in the 1960s–1970s at Peninj, near Lake Natron in Tanzania, in the Omo River basin of southern Ethiopia, and at Koobi Fora, east of Lake Turkana, Kenya, populated the Plio-Pleistocene fossil record of eastern Africa with crania, jaws, and teeth of a hominin whose morphological pattern was easily accommodated in the adaptive mold of Robinson's vegetarian *Paranthropus* (Robinson 1960). Most workers have since upheld separate species status for these hominins (as *P. boisei* or *A. boisei*) on the grounds of morphological distinction and/or geographical separation (Tobias 1967; Howell 1978; Rak 1983).

The identification in 1964 of *Homo habilis* approximately contemporaneous with OH 5 at Olduvai Gorge (in Bed I, ca. 1.8 Ma) recalled the earlier discovery of "true man" (*Telanthropus capensis*) alongside *Paranthropus* in the pink breccia (later Member 1) at Swartkrans (Broom and Robinson 1949; Robinson 1953b; Leakey et al. 1964). Robinson (1965 et seq.) dismissed the Bed I *H. habilis* fossils as an east African variant of *A. africanus*, which he believed was ancestral to modern humans, while advocates of the "single species hypothesis" struggled to accommodate all southern and eastern African hominin morphological diversity within single evolving species (Brace 1967; Wolpoff 1970). However, the recovery of a cranium of *Homo erectus* (KNM-ER 3733) in the same radioisotopically dated horizon (ca. 1.75 Ma) of the Koobi Fora Formation (Kenya) that yielded *A. boisei* (e.g., KNM-ER 406) validated once and for all the idea that the pattern of early human evolution was, at least partly, the result of a process of diversification through speciation rather than a linear process of morphological advancement (Leakey and Walker 1976).

The Leakeys' argument for a geologically early appearance of genus *Homo*, bolstered by the 1972 recovery of the relatively large-brained, flat-faced KNM-ER 1470 (initially dated erroneously to >2.6 Ma but now known to be ca. 1.9 Myr old), strongly influenced the first interpretations of fossil hominin diversity in the collections made during the 1970s in pre-3.0-Myr-old sediments at Hadar and Laetoli. While the small Laetoli sample was thought to contain an early precursor of *Homo* (Leakey et al. 1976), as many as three hominin taxa, including one similar to the Laetoli form, were believed to inhabit the Hadar assemblage of teeth, jaws, and postcrania (Johanson and Taieb 1976). Such early diversity made sense given the Robinsonian view of an *A. africanus*-like ancestor for a geologically old *Homo* lineage, implying earliest Pliocene or even late Miocene hominin cladogenesis (Tobias 1973).

By the late 1970s, the correct allocation of KNM-ER 1470 to the latest Pliocene and the reinterpretation of the Hadar and Laetoli fossils as representing a single species (Johanson and White 1979) had refocused discussion around two different two-lineage models, both of which featured *A. afarensis* at the root of mid-Pliocene hominin diversity. One, a twist on Robinson's diet-driven diversity scenario, envisioned *A. africanus* as the basal taxon of a "robust" australopith clade, based on the view from the perspective of the craniodentally plesiomorphic *A. afarensis* of derived masticatory morphology in the hominins from Sterkfontein, Makapansgat, and Taung (White et al. 1981; Rak 1983; Kimbel et al. 1984). The other interpreted *A. africanus* as the better candidate for the common ancestry of *Homo* and "robust" australopiths by virtue of their shared derived morphology in the premolars and canines, mandible, and calvaria relative to more plesiomorphic states in *A. afarensis* (Kimbel et al. 1984; Skelton et al. 1986), but with implied reversals in derived states inferred to be related to heavy chewing in the transition to *Homo*.

Underscoring an emerging consensus on the importance of cladogenesis in the early record of human evolution, homoplasy became a dominant theme in paleoanthropological writings on australopith systematics during the 1980s. These focused in particular on the likelihood of independent evolution of skeletal responses to heavy mastication (see contributions in Grine 1988), an issue highlighted by the discovery of the 2.5-Myr-old KNM-WT 17000 cranium attributed to *A. aethiopicus* (Walker et al. 1986), whose startlingly plesiomorphic attributes within an otherwise fairly typical "robust" australopith anatomical milieu ensured a high degree of homoplasy (in the masticatory apparatus or cranial base) in any phylogenetic hypothesis that attempted to accommodate all australopith (and early *Homo*) species then known (Kimbel et al. 1988). *A. africanus*, more than any other species, continued to occupy a place of uncertainty in hominin phylogeny, which led to musings on whether the type species of the genus may actually comprise more than one species taxon (Clarke 1988, 1994; Kimbel and White 1988; Kimbel and Rak 1993) – a view that remains in the minority, despite the uncommon degree and type of cranial and dental morphological variation within the now 700+ specimen Sterkfontein sample.

The 1990s was a decade in which a great deal of paleoanthropological field work concentrated on extending the record of early hominins into the late Miocene, the period in which the evidence from DNA pinpoints the divergence of chimpanzee and human lineages. At least five hominin taxa predating *A. afarensis* have been recognized since 1994 (*Ardipithecus kadabba, A. ramidus, Orrorin tugenensis, Sahelanthropus tchadensis, A. anamensis*), aggregately spanning the period between ca. 4.2 and ca. 6–7 Ma. Relative to *A. afarensis*, all are more plesiomorphic in dental, mandibular, and cranial morphology. The youngest, *A. anamensis*, is by far the most similar morphologically to *A. afarensis* and subsequent australopiths (Leakey et al. 1995; Ward et al. 2001). For the purposes of this chapter, the australopiths will be taken to include *A. anamensis* as their earliest known representative.

Other recently proposed taxa in the 2–4-Myr time range, including *A. garhi* from Ethiopia (Asfaw et al. 1999), *A. bahrelghazali* from Chad (Brunet et al. 1996), *Kenyanthropus platyops* from Kenya (Leakey et al. 2001), and a so far undiagnosed form from Member 2 at Stertkfontein, South Africa (Clarke 2002), hint at as yet poorly understood aspects of hominin diversity and geographical distribution in the early to middle Pliocene of Africa. They will be mentioned in the survey of australopith species provided below, but relatively little is known about them compared to the other species included in the group. Table 2 lists the australopith species that will be discussed in this survey.

Table 2 Australopith species diversity according to nominal taxa

Taxon	Geographical distribution	Known age range (Ma)
Australopithecus africanus Dart 1925	South Africa	ca. 3.0–2.0
Australopithecus sediba Berger et al. 2010	South Africa	ca. 2.0
Australopithecus robustus (Broom 1938)	South Africa	ca. 1.5–2.0
Australopithecus boisei (Leakey 1959)	Tanzania, Kenya, Ethiopia, Malawi	≥2.3–1.4
Australopithecus afarensis Johanson et al. 1978	Ethiopia, Tanzania, Kenya	≥3.8–3.0
Australopithecus aethiopicus (Arambourg and Coppens 1968)	Ethiopia, Kenya, Tanzania	ca. 2.7–2.3
Australopithecus anamensis Leakey et al. 1995	Kenya	4.2–4.0
Australopithecus garhi Asfaw et al. 1999	Ethiopia	2.5
Kenyanthropus platyops M.G. Leakey et al. 2001	Kenya	3.5

Systematic Context of Australopith Diversity

Morphological diversity, taxonomic diversity, and species-lineage diversity do not neatly map onto one another in paleontology. This is largely due to the entrenched use of a phenetic species concept in this science, which tends to endorse the recognition of lineage segments as species. But the delineation of the "actors" in evolutionary processes over geological spans of time requires that we move beyond the recognition of "paleospecies" as static phenetic constructs, useful only as a formal catalogue of diversity, to rendering them as close to the entities that underpin the notion of the genetic species as lineages evincing signs of a unique network of gene exchange (see Kimbel and Rak 1993 for discussion and references). Substantial change can in principle accrue in such lineages under a model of anagenesis – amounts that would prompt many paleontologists to recognize distinct paleospecies at widely separated temporal cross sections of a lineage – but, in the absence of cladogenesis, no actual increase in lineage diversity would have resulted from this process. Therefore, to understand the diversity of australopiths, it is one thing to identify and name morphologically distinct taxa and quite another to delineate species lineages. Although a morphologically diagnosed species and a species lineage may exactly coincide, where fossil samples with different morphologies and temporal distributions are involved, the identification of species lineages entails a complex analytical process involving the comparison of phylogenetic hypotheses based on polarized morphological character states (cladistics) with data on the temporal distribution of form (stratophenetics). Where these approaches yield the same character transformations, with minimal stratigraphic gaps and no autapomorphies in temporally intermediate samples, the simplest explanation of the observed data may be the existence of a temporal sequence of samples representing ancestral and descendant populations within a single lineage (Smith 1994) even if two or more distinct nominal species are thereby joined in one *evolutionary species* (Simpson 1951; Wiley 1978; Krishtalka 1993). There is always the possibility that the evidence for an anagenetic lineage may mask a poorly resolved record of cladogenesis. Accordingly, a fairly densely sampled fossil record over a well-calibrated stratigraphic record and a reasonably complete sampling of taxa from the relevant time period are necessary for this kind of analysis. These requirements are rarely met in the hominin fossil record (but see Wood et al. 1994 and Kimbel et al. 2006 for exceptions).

In the following survey, I examine australopith diversity as a record of nominal taxa as well as attempting to characterize it in terms of species lineages. Because I am concerned with taxonomic diversity, my review focuses on craniodental morphology.

Species Diversity of Australopiths

Australopithecus anamensis (M. Leakey et al. 1995)

Known temporal distribution: ca. 4.17–3.95 Ma, based on radioisotopic age determinations on tephras (Leakey et al. 1995, 1998).

Known geographical distribution: Kanapoi, southwest of Lake Turkana, and Allia Bay, east of Lake Turkana, Kenya (Koobi Fora Formation); Asa Issie and Aramis sites, Middle Awash valley, Ethiopia.

Holotype: KNM-KP 29281, adult mandible with complete dentition and associated temporal bone fragment from Kanapoi.

Hypodigm: Seventy-eight catalogued fossils have come from the Kanapoi site (including the distal humerus reported by Patterson and Howells 1967); 31 specimens have come from Allia Bay (Ward et al. 2001, 2013). The combined sample comprises mostly dentognathic specimens, including, from Kanapoi, three adult mandibles, an adult maxilla, and deciduous and permanent teeth; from Allia Bay, an adult mandibular fragment, two fragmentary adult maxillae, and deciduous and permanent teeth. Postcranial material includes a distal humerus, a capitate, a proximal hand phalanx, and associated proximal and distal portions of a tibia from Kanapoi. Fragments constituting most of an adult radius from Sibilot Hill (Heinrich et al. 1993), ca. 20 km from the main fossil-bearing locality at Allia Bay, have been attributed to the species based on its inferred geological age (Ward et al. 2001). Additional teeth, a fragmentary maxilla, and a femoral shaft, representing no fewer than eight individuals, have been recovered from Asa Issie and Aramis, in the Middle Awash valley of Ethiopia (White et al. 2006).

Diagnostic morphology: Craniodentally, *A. anamensis* differs from extant African apes and Mio-Pliocene hominins (such as *Ardipithecus* and *Sahelanthropus*) chiefly in its expanded postcanine dental battery, including occlusally more complex premolars and thicker cheek tooth enamel, characteristics that are shared with later australopiths and early *Homo*. In morphology and functional wear, *A. anamensis* canines are less apelike than those of earliest known hominins (i.e., *Ardipithecus kadabba*; Haile-Selassie et al. 2004).

Differences from *A. afarensis* and later australopiths pervade the dentition, mostly in the anterior arcade, as well as in the symphyseal region of the mandible and the nasal region of the maxilla. The lower lateral incisors are mesiodistally expanded, as are the lower third premolars and maxillary canines. The P_3 is more asymmetric in occlusal form and is uniformly single-cusped, with an incipient metaconid expressed as a tiny pyramidal expansion of the transverse crest rather than a fully developed cusp, and it usually has a relatively large, mesiolingually "open" anterior fovea. Maxillary canine crowns are symmetric in lateral view, with basally positioned mesial and distal shoulders. Although canine crown size is approximately equivalent to that of *A. afarensis*, the canine roots in *A. anamensis* are considerably larger than in this younger australopith species (Ward et al. 2010, 2013). The buccolingually compressed and occlusally simple deciduous first molar crown differs from the more fully molarized dm_1 of subsequent australopiths and recalls the apelike form of this tooth in *Ardipithecus*.

Mandibles (KNM-KP 29281, KNM-KP 29287, KNM-KP 31713) feature an externally convex anterior corpus and a strongly inclined, retreating symphyseal cross section with a "cut away" basal segment, which is manifested in a marked inferomedial inflection of the lower lateral corpus in the canine/premolar region. The lower canine crown is set lateral to the long axis of the postcanine tooth row, giving the dental arch a long, rectangular shape that is reflected in the nearly parallel-sided maxillary dental arch. However, based on what little is actually preserved of the midline cross section, the reconstructed dental arch in the maxilla KNM-KP 28283 is too narrow and posteriorly convergent as depicted in published photographs (e.g., Leakey et al. 1995, Fig. 1b; partly corrected in Ward et al. 2001, Fig. 3). In the maxilla (KNM-KP 29283 from Kanapoi, ARA-VP 14/1 from the Middle Awash), large canine roots shape the morphology around the nasal aperture. The lateral margins of the aperture are rounded, not sharp as in *A. afarensis*, and the inferior margin is indistinct, with the subnasal surface arching smoothly into the nasal cavity.

A single fragmentary temporal bone (KNM-KP 29281) forms part of the holotype. From a small, evidently female individual, it has a flat mandibular fossa with an indistinct articular eminence and a horizontally disposed, shallow, and sagittally convex tympanic element that extends laterally to a small-diameter external auditory meatus. Although each of these features can be found individually among *A. afarensis* temporal bones from Hadar, their strong apelike expression in combination is not encountered in the Hadar sample.

The tibia and hand phalanx from Kanapoi, and the radius from East Turkana (granting its assignment to *A. anamensis*), are very similar to other australopith homologues, and the tibia constitutes the earliest known skeletal evidence for australopith bipedality. The capitate (KNM-KP 31724) is distinctive, however, in the relative orientation of the distal facets for the second and third metacarpals. As in great apes, but unlike the condition in later australopiths and humans, the facet for MC II is laterally directed and set at approximately 90° to the facet for MC III, implying little or no rotational capability at the carpal/MC II joint (Leakey et al. 1998).

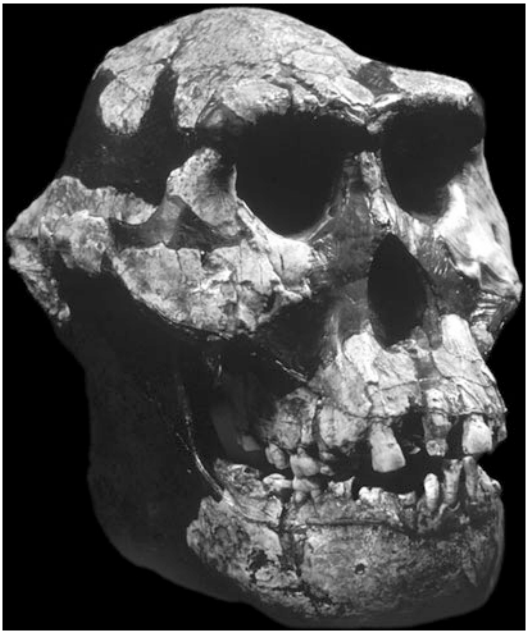

Fig. 1 Three-quarters view of the reconstructed skull of *A. afarensis* specimen A.L. 444-2 from Hadar, Ethiopia (Photo by W. Kimbel and Y. Rak)

Discussion: The *A. anamensis* hypodigm presents a distinctive and significantly more apelike anatomical package than those of subsequent australopith species. However, when the sample is separated into subsamples by site, a more complex picture emerges. Although the younger sample from Allia Bay is much smaller and less representative anatomically than the one from Kanapoi, in several of its morphological details, it stands out relative to conditions in the latter sample (Kimbel et al. 2006). The Allia Bay P_3 (in mandible KNM-ER 20432) has an expanded posterior fovea, and its anterior fovea is partly sealed by an elevated mesial marginal ridge. The mandible corpus fragment in which this tooth is preserved does not appear to possess the inferomedial inflection of the lateral corpus under the premolars, implying a less retreating symphyseal cross section. The Allia Bay lower canines ($n = 2$) show less development of the distal cingulum than in the Kanapoi sample ($n = 4$). These distinctions of the Allia Bay sample are the most common states in *A. afarensis* and bridge *A. anamensis* to that taxon. Moreover, as suggested initially by Leakey et al. (1995), the differences between *A. anamensis* and *A. afarensis* are not as pronounced when the geologically older Laetoli sample of *A. afarensis* is considered separately from the younger sample from Hadar (see below, under *A. afarensis*). In fact, the hypothesis of anagenetic change efficiently accounts for the observed morphological transformations across the four temporally ordered site samples, implying that *A. anamensis* and *A. afarensis* constitute a single evolutionary species (Kimbel et al. 2006; see also White et al. 2006).

Key references: Haile-Selassie et al. 2004; Kimbel et al. 2004, 2006; Leakey et al. 1995, 1998; Ward et al. 2001, 2013; White et al. 1994, 1995, 2006.

Australopithecus afarensis (Johanson et al. 1978)

Known temporal distribution: ca. 3.8–3.0 Ma based on radioisotopic age determinations on tephras, supported by biochronology and paleomagnetic polarity.

Known geographical distribution: Laetoli, Tanzania (upper Laetolil Beds); Hadar, Ethiopia (Sidi Hakoma, Denen Dora, and Kada Hadar Members, Hadar Formation); Dikika, Ethiopia (Basal Member and Sidi Hakoma Members, Hadar Formation), Woranso-Mille, Ethiopia, Maka, Middle Awash, Ethiopia ("Maka Sands," Matabaietu Formation), East Turkana, Kenya (Tulu Bor Member, Koobi Fora Formation), possibly Koro Toro, Bahr-el-Ghazal, Chad.

Holotype: LH-4, mandible with dentition, from upper Laetoli Beds, Laetoli, Tanzania.

Hypodigm: Approximately 90 % of the hypodigm of *A. afarensis* comes from Hadar Formation sediments exposed at the Hadar site in Ethiopia ($n = 367$ specimens). The Hadar sample includes two partial skeletons with craniodental associations (A.L. 288-1, A.L. 438-1), two nearly complete (A.L. 444-2, A.L. 822-1) and one partial (A.L. 417-1) skull, 57 adult or subadult mandibular portions, 13 adult or subadult maxillae, 12 calvarial specimens (including a partial juvenile cranium, A.L. 333-105), and a wealth of upper limb, lower limb, and axial material, the majority of which comes from the A.L. 333 locality (see descriptive papers in the March 1982 *American Journal of Physical Anthropology* and Latimer et al. 1987; Latimer and Lovejoy 1989, 1990a, b; Kimbel et al. 1994, 2004; Drapeau et al. 2005). The Laetoli site sample consists of the holotype mandible (LH-4), several adult or subadult jaws (Garusi I, LH-2, LH-5), a fragmentary partial skeleton of a juvenile (LH-21), and an assortment of teeth (White 1977, 1980, 1981). Trace fossils in the form of the Laetoli bipedal hominin footprint trails, presumed to have been made by *A. afarensis*, are part of the species' hypodigm. From the Maka site in Ethiopia have come a proximal femur, a humerus, and several jaws, including a nearly complete mandible, at 3.4 Ma (White et al. 1993, 2000; Lovejoy et al. 2002). A partial calvaria (KNM-ER 2602; Kimbel 1988) is known from Koobi Fora. Although the 3.0–3.5-Myr-old mandible fragment (KT-12/H1) from Koro Toro, Chad, has been made the holotype of *A. bahrelghazali* by Brunet et al. (1996), its anatomy does not appear to distinguish it from the range of variation encompassed by the Hadar/Maka mandibular series, and so it is here tentatively interpreted to extend the geographical distribution of *A. afarensis* into north-central Africa. The Middle Awash frontal fragment from Belohdelie may also belong to *A. afarensis*, which would extend the time range of the species back to ca. 3.9 Ma (Asfaw 1987; Kimbel et al. 2004).

Diagnostic morphology (Fig. 1): *A. afarensis* can be distinguished from *A. anamensis* by a more molarized, symmetric P_3 crown with more frequent development of the second cusp (metaconid) and transverse orientation in the tooth row; an asymmetric upper canine with more apically positioned mesial crown shoulder; a molarized dm_1 with buccolingually expanded talonid; a straighter, commonly more upright anterior corpus profile, with a "filled out" basal segment and little to no inferomedial inflection of the lower corpus beneath the canine-premolars; lower canines set medial to postcanine row axis; a wider palate at equivalent palate lengths; a nasal aperture defined by sharp lateral margins and distinct inferior margin, with the canine jugum a distinct entity in the circumnasal topography; and a larger external auditory meatus. In all of these features, *A. afarensis* exhibits the derived condition for hominins.

Compared to all subsequent australopiths, a distinctive, predominantly plesiomorphic, anatomy pervades the *A. afarensis* skull and dentition. The calvaria testifies to an extensive posterior *m. temporalis* origin, with posteriorly extended sagittal crests and compound temporal/nuchal crests in both large (putatively male) and small (putatively female) specimens. The nuchal plane of the occipital bone is transversely convex and set at a steep angle to the Frankfurt plane, especially in less heavily crested small and subadult individuals, and it transitions to a relatively short occipital plane. In some individuals the nuchal plane extends superiorly to a very high position on the rear of the braincase. The cranial base features a shallow mandibular fossa bounded anteriorly by a weak to moderately developed articular eminence and posteriorly by an inflated postglenoid process that sits anterior to the tympanic element. The tympanic is a horizontally inclined tube, rather than a vertically oriented plate, and it usually lacks a distinct crista petrosa. Venous blood outflow was predominantly through the occipital-marginal rather than through the transverse-sigmoid sinus system. The frontal bone features a low, flat to mildly convex squama lacking a frontal trigone, coronally oriented, laterally thickened supraorbital bars, and broad postorbital breadth relative to other facial breadth dimensions. The midfacial axis (nasion-nasospinale) is upright, in contrast to the strongly projecting, convex subnasal plane (nasospinale-prosthion), which protrudes anteriorly beyond the bicanine line (also seen in *A. garhi*). Interorbital and nasal aperture breadths are narrow, contrasting with the broad, flat, and massive zygomatic region. The maxilla's zygomatic process root is located above M^1 or P^4-M^1, and its inferior margin is moderately to strongly arched. Within the nasal cavity, an elevated platform separates the inferior nasal margin from the anterior vomeral insertion. The palate is moderately deep in narrow jaws but is shallower in wider ones, and the upper dental arch is subparallel with slight convergence to moderate divergence posteriorly. The mandible has a deep but relatively thin corpus at the molars, and a moderately tall ramus originating high on the corpus and separated from it by a narrow extramolar sulcus. In individuals with an associated mandible and maxilla (i.e., A.L. 417-1, A.L. 444-2, A.L. 822-1), the mandibular corpus constitutes more than two-thirds of the orbitoalveolar height in the coronal plane of the orbits. The external contour of the anterior corpus is full and transitions to a vertical lateral corpus beneath the canines and premolars. Although the symphyseal axis is more vertical than in *A. anamensis*, it is, on average, less vertical than in subsequent australopiths. The lower anterior dental arch is pinched in small mandibles but widens into a U-shape in larger specimens, perhaps under the influence of moderate canine dimorphism.

Most of the distinctive dental features of *A. afarensis* are focused in the canines and premolars, which in this species are captured in evolutionary transition. Molarization of the P_3 is less advanced than in subsequent australopiths: the metaconid is variably expressed, with some individuals primitively lacking a distinct second cusp (e.g., A.L. 128-23, 277-1, 288-1, 417-1), though these are not necessarily those with a more "apelike" skewed occlusal outline and oblique orientation in the tooth row. Absolute canine size overlaps that of *A. africanus*, though relative to postcanine size the *A. afarensis* canines are larger. Some canines reveal ancestral traces of shearing wear (e.g., on the elongated distal crests of the lower), which is lost almost entirely in subsequent australopith species, but this is significantly less developed than in *A. anamensis* and especially *Ardipithecus*, and occlusal wear in *A. afarensis* canines and premolars is predominantly apical. Nevertheless, in some mandibles canine and mesial P_3 crowns stand tall even in the face of extreme occlusal molar wear, a remnant of the ancestral occlusal wear pattern.

Discussion: Well-documented variation in the large *A. afarensis* sample from Hadar indicates high levels of cranial polymorphism. Some of this variation is due to sexual dimorphism in size and shape, while some of it is due to anagenetic trends in craniodental morphology during the younger half (3.5–3.0 Ma) of the *A. anamensis* to *A. afarensis* species lineage (Lockwood et al. 2000). The Laetoli sample (ca. 3.8–3.6 Ma) figures prominently in this discussion. Although some dental metric differences between the Laetoli and Hadar samples have been cited in the past (White 1985), it now appears that the metric and morphological differences between the hominin populations represented at these sites are phylogenetically significant. Despite limited samples, the convex, retreating form of the adult anterior mandibular corpus (LH-4), mirrored in that of a juvenile (LH-2); the influence of the canine root on the curved lateral margin; the indistinct inferior margin of the nasal aperture (Garusi I); and the mesiodistally expanded lower canine and P_3 crowns recall conditions diagnostic of *A. anamensis* and occur in more derived states in the Hadar sample (Kimbel et al. 2006). The recently recovered sample of teeth and jaws from Woranso-Mille, dating to ca. 3.6–3.8 Ma, reinforces the hypothesis of dentognathic evolution along the *A. anamensis* to *A. afarensis* lineage (Haile Selassie et al. 2009).

Later in time, in the Kada Hadar Member at Hadar (ca. 3.0–3.1 Ma), there is evidence of an anagenetic increase in hominin skull size (and perhaps body size), which drove the *A. afarensis* mandibular corpus and facial skeleton to sizes rarely encountered in older strata (Lockwood et al. 2000). This trend was not accompanied by especially large postcanine teeth, more robust mandibular corpora (i.e., thicker in relation to depth), or by anteriorly shifted masticatory muscle blocks that are usually thought to signal diet-related morphological specializations in subsequent species of the australopith group. The causal processes underlying the observed increase in size are presently unclear, but it does roughly correspond to a change in the Hadar mammalian faunal community to more arid-adapted taxa (e.g., among the bovids).

The Burtele site, in the Woranso-Mille area of Ethiopia, has yielded a fossil partial foot skeleton from sediments contemporary with the Sidi Hakoma Member at Hadar and Dikika (ca. 3.4 Ma; Haile-Selassie et al. 2012). This specimen features a divergent hallux, which is universally present in arboreal catarrhines. However, derived features, including the dorsally “domed” heads of the lateral metatarsals and the anterior cant of the corresponding phalangeal bases, suggest toe off in terrestrial bipedality, as in *Australopithecus* and *Homo*. The mix of primitive and derived morphology in the Burtele foot, matching that of early Pliocene *Ardipithecus ramidus*, is strong evidence for a second species lineage contemporary with *A. afarensis* in eastern Africa (Haile-Selassie et al. 2012).

Key references: Alemseged et al. 2005; Drapeau et al. 2005; Haile Selassie et al. 2009, 2012; Kimbel and Delezene 2009; Kimbel and Rak 2010; Kimbel et al. 2004, 2006; Lockwood et al. 2000; White et al. 2003; papers in *American Journal of Physical Anthropology*, Vol. 57, 198.

Kenyanthropus platyops (M.G. Leakey et al. 2001)

Known temporal distribution: ca. 3.3–3.5 Ma based on radioisotopic dating of tephra.

Known geographical distribution: Lomekwi (Nachukui Formation), west of Lake Turkana, Kenya.

Holotype: KNM-WT 40000, a crushed and distorted cranium with partial dentition.

Hypodigm: In addition to the holotype, a partial maxilla with dentition (KNM-WT 38350). (Other hominin fossils, including a partial temporal bone, a mandible fragment [formerly attributed to *A. afarensis* by Brown et al. (1993)], and some isolated teeth, were withheld from attribution to this taxon by Leakey et al. (2001).)

Diagnostic morphology: While enumeration of the diagnostic features of *K. platyops* is hampered by poor preservation of the holotype, taphonomy does not appear to account for all of the distinctive morphology of the type cranium relative to that of known specimens of *A. afarensis*, with which it was contemporary (Spoor et al. 2010). These differences reside mainly in the lower part of the face (Leakey et al. 2001) and include an anteriorly positioned root of the maxillary zygomatic process (above P^3-P^4, and seen in both the type specimen and KNM-WT 38350) and a transversely and sagittally flat subnasal plane with minimal projection beyond the canines. In addition, the dominant venous outflow track was via the transverse-sigmoid system, in contrast to the occipital-marginal system, which is very common in *A. afarensis* (though the Laetoli juvenile LH-21 also evinces the transverse-sigmoid drainage route). The size of the external auditory meatus is smaller than that of *A. afarensis*, despite the latter’s extensive variation in this feature (Kimbel et al. 2004), and approaches the tiny EAM of *Ardipithecus ramidus* and *A. anamensis*. The second molar in the type cranium is much smaller than that of other australopith M^2s, while the M^1 of KNM-WT 38350 is also very small.

Discussion: Along with the Burtele foot (see above), the specimens attributed to *K. platyops* currently constitute the best evidence for hominin lineage diversity prior to 3.0 Ma. On the basis of published information (Leakey et al. 2001), the material attributed to *K. platyops* shares only primitive characteristics with

A. afarensis (e.g., tubular tympanic element lacking a petrous crest, posteromedially angled temporal lines and an emphasis on posterior cranial crests, low and curved zygomaticoalveolar crest), but its facial configuration appears more derived than what is observed in the large cranial sample of that species. None of these derived characteristics are observed in the sample of one dozen adult maxillae in the Hadar sample of *A. afarensis*, or in the Garusi maxilla from Laetoli, which is demonstrably more primitive in the circumnasal region than the Hadar specimens (as discussed above and in greater detail in Kimbel et al. (2006)) yet is the more precise chronological match for the *Kenyanthropus* holotype. (KNM-WT 38350 is approximately contemporary with Hadar specimens A.L. 417-1, A.L. 200-1, and others from the middle Sidi Hakoma Member.) Therefore, *K. platyops* sits in phylogenetic isolation. There are no shared derived characters linking it to the *A. anamensis* to *A. afarensis* species lineage, and although favorable comparisons have been made directly with the lower facial morphology of *Homo rudolfensis* (i.e., KNM-ER 1470), at ca. 2.0 Ma (Leakey et al. 2001), it is unrealistic to link these two specimens via a meaningful phylogenetic hypothesis given 1.5 myr of no intervening data.

Key references: Leakey et al. 2001; Spoor 2010.

Australopithecus africanus (Dart 1925)

Known temporal distribution: ca. 3.0–2.0 Ma, based on U/Pb dating, paleomagnetic polarity and biochronological correlations with radioisotopically calibrated sequences in eastern Africa (Herries et al. 2013).

Known geographical distribution: Taung, Sterkfontein, and Makapansgat, South Africa.

Holotype: Juvenile skull, dentition, and endocast from Taung.

Hypodigm: In addition to the holotype, crania, jaws, teeth, and postcrania from Sterkfontein and Makapansgat. The Sterkfontein sample is by far the more extensive, consisting of some dozen nearly complete or partial crania (e.g., TM 1511, Sts 5, 17, 71, Stw 13, 505) and adult and juvenile mandibles plus hundreds of teeth, in jaws or isolated. Numerous postcranial remains are known, including at least three partial skeletons (Sts 14, Stw 431, Stw 573: Toussaint et al. 2003), but only one (Stw 573) is definitively associated with taxonomically diagnostic craniodental remains. The Makapansgat sample comprises roughly 40 specimens, including several jaws (MLD 2, 6/23, 9, 18, 40), two partial adult calvariae (MLD 1, MLD 37/38), and some fragmentary cranial and postcranial elements.

Diagnostic morphology (Fig. 2): Compared to *A. afarensis*, *A. africanus* has a higher, shorter braincase with rare sagittal cresting and no compound temporonuchal cresting. The supraorbital torus thins laterally from top to bottom and is occasionally divided into distinct supraorbital and superciliary components (Lockwood and Tobias 1999). The cranial base is a bit narrower in absolute terms, but in relation of calvarial size, it is broader and shorter than in apes. The occipital plane of the occipital bone is higher and the nuchal plane is flatter and more

Fig. 2 Oblique views of Sterkfontein *A. africanus* crania Sts 71 (*left*) and Sts 5 (*right*) (Photo by W. Kimbel and Y. Rak)

horizontally inclined. The mandibular fossa is deeper on average, with a stronger articular eminence. The tympanic element is more vertically oriented, usually bears a distinct crista petrosa, and tapers medially to a distinctive Eustachian process. Venous drainage from the endocranium is predominantly through the transverse-sigmoid system. Prominent anterior pillars border the nasal aperture, even in young individuals, and the subnasal plate is flat to slightly convex sagittally and much less projecting relative to the bicanine axis. Within the nasal cavity, the step-down to the nasal floor and anterior vomeral insertion occurs immediately posterior to nasospinale, usually without an intervening platform. The zygomatic bone features a variably prominent boss at the transition to the temporal process and a strong sagittal inflection across the frontal process/facial surface transition, which combine to create a central facial hollow in some individuals (e.g., MLD 6/23, TM 1511, Sts 71, Stw 505). Zygomatic process roots typically originate more anteriorly (above P^4/M^1 to P^4/P^3) and have a straight, superolaterally diverging inferior margin. The palate is, on average, deeper, with an inferiorly flexed premaxillary segment and posteriorly divergent tooth rows. The mandible corpus is more robust (breadth as a percentage of depth at M_1) and has a more inflated lateral surface beneath the premolars and a straighter, more vertical symphyseal profile. Dentally, compared with *A. afarensis*, *A. africanus* has absolutely larger (especially broader) postcanine teeth with centrally crowded molar cusp apices in some individuals. The P_3 is uniformly bicuspid, canine wear is exclusively apical, and the anterior-posterior adult occlusal wear gradient is weaker. C/P_3 and I^2/C diastemata are less frequent.

In its moderate (though impressively variable) upper midfacial prognathism (nasion-nasospinale), occasionally patent premaxillary suture in adult faces, and less topographically complex glenoid region of the temporal bone, *A. africanus* remains plesiomorphic in relation to *A. robustus* and *A. bosei* (but not *A. aethiopicus*). The mandibular corpus is less robust compared to states observed in *A. aethiopicus*, *A. robustus*, and *A. boisei*, and dental size and the anterior-posterior tooth row proportions remain relatively conservative (especially those involving the premolars, which are less expanded in relation to the molars). Facial breadths are narrower as a percentage of calvarial breadths, giving the impression that the cranium is less constricted postorbitally, though the minimum frontal breadth dimension is of similar absolute magnitude. The vertex of the braincase (in specimen Sts 5 at least) is higher in relation to the orbital roof when compared to crania of *A. aethiopicus, A. robustus*, and *A. boisei* (as well as *A. afarensis* and the great apes), but when size-standardized by calvarial length, vertex height is greater only than that of the "robust" species.

Discussion: The large *A. africanus* sample from the Sterkfontein Member 4 ("type site") fossil assemblage is notable for its unusually extensive range of craniodental variation (e.g., basal aspect of the temporal bone, facial topography and subnasal prognathism, postcanine tooth size), which has led to proposals that more than one hominin species may be contained within it (Clarke 1988, 1994, 1998; Kimbel and White 1988; Kimbel and Rak 1993; Moggi-Cecchi et al. 1998; Lockwood and Tobias 2002). However, because dividing the sample to create overlapping cranial and dental morphs has proven difficult (while different authors tend to disagree on such divisions in the first place), these proposals have not attracted much support (see Grine 2013 for a review). Still, appeals to normal sources of variation within a single geographically delimited biological species (chiefly sexual dimorphism) do not account for the variation, as much of this does not follow patterns of dimorphism observed within extant catarrhine species (Kimbel and White 1988; Kimbel and Rak 1993). The lack of chronological control within the Member 4 faunal assemblage leaves open the possibility that the hominin sample is time-transgressive. Kimbel (1986) offered as an explanation for the Sterkfontein Member 4 variation the temporal mixing of individual organisms' remains from morphologically distinct populations of *A. africanus* that had moved in and out of the Sterkfontein valley over a long period of time. Although Kuman and Clarke's (2000) revised stratigraphy implies a long and complex depositional history for Member 4, this idea is difficult if not impossible to test and does not in any event preclude the inclusion of fossils from more than one hominin species in the Member 4 sample. The basic systematics of the type species of *Australopithecus* remains a vexing issue, and the likelihood of being able to discern lineages is remote.

More recently, excavations in previously unexploited depositories in the Sterkfontein cave system have led to discoveries of hominin fossils originally said to be significantly older (ca. 4 Ma) than *A. africanus* of Member 4 (Clarke 1988, 2002; Partridge et al. 2003). These remains include a partial skeleton and skull (Stw 573) still being excavated in situ in the Silberberg Grotto and a small collection of specimens, including fragments of an adult cranium (Stw 578), from Jacovec Cavern. Published reports suggest general australopith affinities for these specimens. While their exact antiquity is uncertain, in part due to an extremely complex stratigraphic context, Herries et al. (2013) have presented evidence that these deposits are contemporaneous with Member 4 of the Sterkfontein site (ca. 2.0–2.6 Ma).

Key references: Broom and Schepers 1946; Broom et al. 1950; Robinson 1956; White et al. 1981; Rak 1983; Clarke 1994; Lockwood and Tobias 1999, 2002; Grine 2013.

Australopithecus sediba (Berger et al. 2010)

Known temporal distribution: Faunal, paleomagnetic, and U/Pb dating methods combine to suggest a ca. 2.0 Ma age for the fossil-bearing sedimentary infill in the Malapa cave system, South Africa (Berger et al. 2010; Pickering et al. 2011; Herries et al. 2013).

Known geographical distribution: Malapa cave system, Gauteng Province, South Africa.

Holotype: MH1, a subadult partial skeleton and skull thought to be male (Berger et al. 2010).

Hypodigm: A subadult's partial skeleton and skull, reportedly male (MH1, the holotype), and an adult's partial skeleton and mandible, thought to be female (MH2). A tibia originally associated with the holotype is now said to represent a third individual (MH3) (Berger 2012).

Diagnostic morphology: The MH1 individual of *A. sediba* is small-brained, with an estimated endocranial volume (ECV) of ca. 420 cc, which must be close to the adult value given that the M^2s had achieved alveolar eruption (Carlson et al. 2011). This single value falls below the mean but within the ranges of *A. afarensis* and *A. africanus* ECV estimates (Holloway et al. 2004). Similarly, canine and postcanine tooth crown dimensions fall in the lower end of the range of size variation for these two australopith species (Berger et al. 2010). The face of MH1 is moderately prognathic with slight subnasal projection, but the latter feature, along with some other putatively diagnostic craniofacial characters, are subject to late growth-related changes. These ontogenetically labile characters include the widely spaced temporal lines, slight relative postorbital constriction, and mild relative lateral flare of the zygomatic arches (the latter two of which are expressed as a percentage of upper facial breadth in Berger et al. 2010). Thus, assessment of fully adult craniofacial shape in *A. sediba* would likely affect comparisons with other australopith species subtly but substantively.

In several respects the MH1 facial skeleton resembles that of *A. africanus* specimen Sts 52a, also a subadult (M3s unerupted). This specimen departs from characteristic *A. africanus* craniofacial anatomy (Rak 1983) in the absence of an anterior pillar, weak subnasal projection, a pronounced canine fossa, and mild eversion of the lateral nasal aperture margins superiorly with consequent slight prominence of the nasal bridge (enhanced by a median keel) – all features observed in MH1. MH1 shares several other craniofacial features with *A. africanus* adults and subadults (including Sts 52a), such as a superiorly placed anterior masseter origin associated with a straight, steeply angled (in anterior view) zygomaticoalveolar crest (Rak 1983; Kimbel et al. 1984).

At first glance, MH1 appears to bear a supraorbital torus separated from the frontal squama by a *sulcus supratoralis*, as in *Homo habilis* (sensu stricto; i.e., excluding fossils often attributed to *H. rudolfensis*). But in *H. habilis* the supraorbital torus is a distinct structure that bulges above the sulcus (with a topographic highpoint that divides the sulcus into lateral and medial sections on each side, as in KNM-ER 1813, OH 16 and OH 24), whereas in MH1 the squama passes onto a shelflike supratoral depression that extends, with little topographic disruption, directly onto the superior surface of the supraorbital structures. Perhaps this difference can be accounted for by the relative youth of MH1, although in hominoids juvenile supraorbital form is typically a good predictor of adult morphology. An alternative interpretation is that the MH1 morphology is one expression of the variable supraorbital form observed in *A. africanus* (as seen in the Sterkfontein Member 4 deposits). In this sample, the supraorbital elements are weakly defined topographically and are separated from the squama by a variably developed depression that ranges from virtually absent (in Sts 71, Stw 505) to mild (Sts 5) to pronounced (TM 1511, as revealed by the impression left in matrix by the specimen's now lost frontal squama; Kimbel and Rak, pers. obs.; see also Plate IV, Fig. 16 in Broom and Schepers 1946). MH1 is similar to the adult TM 1511 in the expression of this morphology (allowing for the effects of age-related differences in temporal line incursion), which is distinct from the *Homo habilis* morphology.

The Malapa mandibles (MH1 and MH2) are small and lightly built, but the extent to which the subadult status of MH1 and the presumptive female status of MH2 present a biased profile of mandibular size and shape variation (which is known to be considerable in other australopith taxa) can only be addressed with additional specimens. Rak et al. (in review) have concluded, however, based on the anatomy of the coronoid notch of the mandibular ramus, that the Malapa sample actually contains two hominin species, one of *Australopithecus* (MH1) and one of *Homo* (MH2) (see Rak et al. 2007).

As in all other australopith species, the *A. sediba* skeleton presents an amalgam of ancestral and derived features. MH2 features a nearly complete hand with a distinctive character mix relative to *A. afarensis*, *A. africanus*, and *H. habilis* (Kivell et al. 2011). The relatively long thumb and short fingers stand out in comparison even to the anatomy of modern humans. A similarly mosaic pattern is said to be found in the pelvis (MH 1 and MH2); it is similar to other australopiths in its large inter-acetabular breadth and long pubis, but distinct from *A. afarensis* and *A. africanus* in having more vertically disposed iliac blades and a shortened ischium (Kibii et al. 2011). Australopith taxonomy has for decades relied chiefly on skull and dental characters (in part because of the rarity of associated craniodental and postcranial remains), so it is noteworthy that the best evidence for the taxonomic distinctiveness of *A. sediba* may come from the postcranium.

Discussion: The case for the specific distinctiveness of the Malapa fossils has been conflated by their discoverers with arguments about its phyletic status (e.g., Berger 2012, p. 4). Neither is helped by the subadult status of the holotype and the fact that its cranium remains (at the time of this writing) partially encased in matrix, obscuring potentially informative portions of the external base (see Carlson et al. 2011). The bulk of the available craniodental evidence, however, argues for a close relationship with *A. africanus* as represented at Sterkfontein Member 4. The *A. sediba* to *A. africanus* relationship may constitute the best evidence for lineage continuity in the Plio-Pleistocene hominin record of southern Africa. If the young age (~2.6–2.0 Ma) of Sterkfontein Member 4 deposits suggested by Herries et al. (2013) is confirmed, then the age of some specimens of *A. africanus* (e.g., Sts 5) may fall within the error range of the age estimate for *A. sediba* at Malapa. Further support for chronological overlap would suggest a sister-group relationship, as opposed to an ancestor-descendant (anagenetic) relationship, between the populations represented by the two site samples.

Berger et al. (2010; Berger 2012) have argued that *A. sediba*, at 2.0 Ma, resided at the base of the *Homo* lineage. But if the unique phylogenetic link between *A. sediba* and *A. africanus* is substantiated, then for this argument to work, *A. africanus* itself would need to be rooted as a sister taxon to the *Homo* clade. Yet most comprehensive phylogenetic analyses of craniodental characters find *A. africanus* to be basal to a strongly supported “robust” australopith-*Homo* clade (e.g., Strait and Grine 2004; Kimbel et al. 2004). The Berger argument also hinges on a dismissal (rather than evaluation) of geologically contemporaneous or older (≥2.0 Ma) fossils from the genus *Homo* (*H. habilis*, *H. rudolfensis*, the A.L. 666-1 maxilla from Hadar, etc.) (Kimbel 2009; Spoor 2011).

Key references: Berger et al. 2010; Carlson et al. 2011; Pickering et al. 2011.

Australopithecus aethiopicus (Arambourg and Coppens 1968)

Known temporal distribution: ca. 2.3–2.7 Ma.

Known geographical distribution: Omo River basin, Ethiopia (Shungura Formation, Members C–F); West Turkana, Kenya (Nachukui Formation); Laetoli, Tanzania (Ndolanya Beds).

Holotype: Omo 18-1967-18, edentulous mandibular corpus (Member C, Shungura Formation, Ethiopia, ca. 2.7 Ma).

Hypodigm: The mostly complete and largely edentulous cranium KNM-WT 17000 from the Nachakui Formation, West Turkana, Kenya (2.5 Ma; Walker et al. 1986; Leakey and Walker 1988) is by far the most complete and well-preserved evidence for this relatively poorly known australopith species. Suwa et al. (1996) assigned to this species some 20 lower postcanine teeth (several in mandibles) from Omo Shungura Formation Members C–F, aggregately spanning ca. 2.7–2.3 Ma. An edentulous maxilla (EP 1500/01) from the Ndolanya Beds at Laetoli has also been assigned to *A. aethiopicus* (Harrison 2002).

Diagnostic morphology: Based on the single known cranium (KNM-WT 17000), *A. aethiopicus* can be distinguished from *A. afarensis* by its extreme midfacial prognathism (nasion-nasospinale); flat subnasal plane; smooth transition from subnasal surface to nasal cavity floor, with indistinct inferior margin of nasal aperture; anterior vomeral insertion and anterior nasal spine merged within nasal cavity; vertically thick palate; anteriorly positioned zygomatic process roots (over P^3/P^4); bulbous, forwardly sloping zygomatic facial surface, which leaves the nasal region in a central facial hollow; low calvarial height; frontal squama with frontal trigone delimited by strongly convergent temporal lines; vertically inclined tympanic element with distinct petrous crest; coronally aligned petrous element; and massive postcanine dentition (inferred from roots and fragmentary P^4 crown; Suwa 1989). Although the KNM-WT 17000 cranium features a very high sagittal crest, its diagnostic value is doubtful, as it was produced by the juxtaposition of enlarged temporalis muscles to a very small braincase (410 cm^3 cranial capacity) that may not have been typical for the species.

The majority of the characters discriminating the *A. aethiopicus* cranium from that of *A. afarensis* link the former species to classical "robust" australopith masticatory configurations. In addition, the dental remains attributed to the former species testify to postcanine size expansion and molarization seen in otherwise only in *A. robustus* or *A. boisei*, though with less premolar crown specialization than in the latter taxon (Suwa 1990; Suwa et al. 1996). However, *A. aethiopicus* retains a number of plesiomorphic characters, such as strong midfacial prognathism, posteriorly accentuated sagittal crest and extensive compound temporonuchal crest, flat mandibular fossa with low, indistinct articular eminence, and (as inferred from roots and alveolar dimensions) relatively large incisors and/or canines. While these characters set *A. aethiopicus* apart from both *A. robustus* and *A. boisei*, they also effectively discriminate it from *A. africanus*, which in several of these respects exhibits derived morphology (cranial vault shape, crest configuration, and mandibular fossa topography).

Discussion: As noted in the historical survey earlier, the discovery of the KNM-WT 17000 cranium provoked discussion about the role of homoplasy in early hominin phylogeny (see contributions in Grine 1988). The fact that aspects of this specimen's cranial morphology are strikingly more plesiomorphic than homologous states in *A. africanus*, combined with its obvious "robust" australopith masticatory signal, implies a high degree of convergent evolution in the australopith skull, the nature of which depends to a large extent on the phyletic position accorded *A. africanus*.

Does the temporal juxtaposition of the morphologically intermediate *A. aethiopicus* between *A. afarensis* and *A. boisei* support the identification of an evolving australopith lineage (evolutionary species) in the Middle to Late Pliocene of eastern Africa? Walker et al. (1986; Leakey and Walker 1988; Walker and Leakey, 1988) thought so and interpreted KNM-WT 17000 as an early, primitive, *A. boisei* specimen. Suwa's (1990; Suwa et al. 1996) detailed analysis of australopith postcanine dental evolution in the Shungura Formation found that in most respects the premolars and molars from Members C–F he attributed to *A. aethiopicus* more closely approximate the generalized condition of *A. robustus* than the highly derived condition of *A. boisei* (e.g., Olduvai Gorge, Koobi Fora, Peninj, etc.), but that the "*A. boisei* morphology emerge[d] in a mosaic fashion across Member G times [i.e., <2.3 Ma]" (Suwa et al. 1996, p. 274), implying in situ evolution of this morphotype. Even so, phylogenetic analyses of cranial morphology have usually identified a monophyletic *A. robustus* + *A. boisei* clade (Strait et al. 1997; Kimbel et al. 2004) whose last common ancestor would be expected to be cranially considerably more derived than the KNM-WT 17000 specimen of *A. aethiopicus*. Thus, given the still spotty fossil evidence in the 2.8–2.3 Ma time interval, the existence of a monophyletic east African "robust" lineage stemming anagenetically from *A. afarensis* remains weakly supported.

Key references: Walker et al. 1986; Leakey and Walker 1988; Grine 1988; Kimbel et al. 1988, 2004; Suwa et al. 1996; Harrison 2011.

Australopithecus garhi **(Asfaw et al. 1999)**

Known temporal distribution: ca. 2.5 Ma based on radioisotopic dating of tephra

Known geographical distribution: Bouri, Middle Awash, Ethiopia (Hata Member, Bouri Formation).

Holotype: BOU-VP 12/130 partial cranium, consisting of frontal, parietal, and maxilla with dentition.

Hypodigm: As for holotype.

Diagnostic morphology: The single specimen of *A. garhi* combines a largely plesiomorphic face and palate with a derived calvarial morphology and a highly unusual hominin dental configuration (Asfaw et al. 1999). It shares with *A. afarensis* a remarkable number of maxillary features including a strongly prognathic, convex subnasal surface; sharp lateral margins of the nasal aperture due to lateral placement of the canine root jugum and lack of anterior pillar; horizontal separation of the vomeral and septal insertions within the nasal cavity; low, arched root of the maxillary zygomatic process; and shallow palate. Although the parietal bones of this apparently male individual bear a fused sagittal crest, it does not exhibit the strong posterior emphasis seen in larger *A. afarensis* crania (e.g., A.L. 333-45, A.L. 444-2). The anterior part of the frontal squama features a depression bounded by the convergent temporal lines, said to be frontal trigone (Asfaw et al. 1999), which is otherwise observed only in *A. aethiopicus*, *A. robustus*, and *A. boisei*.

Dentally, the *A. garhi* cranium combines huge postcanine teeth with large incisors and especially canines. Although postcanine size falls above even the *A. boisei* range, neither enamel thickness nor occlusal form aligns these teeth with "robust" australopiths. The ratio of the calculated crown area of the *A. garhi* P^3 to that of M^2 (70 %, according to data in Asfaw et al. 1999) is greater than that of either *A. afarensis* (mean = 55 %, range = 51–61 %, $n = 5$ individuals with both teeth) or *A. africanus* (mean 54 %, range = 50–61 %, $n = 8$ individuals with both teeth) and even exceeds this ratio in the measurable sample of *A. robustus* specimens (mean = 59 %, range = 52–65 %, $n = 7$), one hallmark of which is relative premolar enlargement. Relative P^4 size (P^4/M^2 ratio = 70 %) is essentially identical to the *A. robustus* mean (69 %). Relative anterior tooth size (as measured by the I^1-C alveolar length as a percentage of the square root of various postcanine tooth crown areas) is smaller than in *A. afarensis* (and in early *Homo*), larger than in *A. robustus* or *A. boisei*, and most similar to that of *A. africanus* (Asfaw et al. 1999).

Discussion: The *A. garhi* cranium presents a unique amalgam of plesiomorphic (*A. afarensis*-like) and derived (*A. africanus*- or "robust" australopith-like) characters. It is similar in this respect to *A. aethiopicus*, although the character combinations are quite distinct in these two contemporary taxa (albeit each represented by only a single cranium). Whereas in *A. aethiopicus* facial and premolar crown forms are the most derived aspects of this species' anatomy (notwithstanding its unparalleled degree of midfacial prognathism), in *A. garhi* it is the morphology of the calotte (including the frontal) and premolar-molar proportions that are apomorphic-maxillofacial morphology remains primitive in this taxon. If we grant that *A. africanus* was approximately synchronic with these species, then this early interval of the late Pliocene presents an impressive and, up to this point in geological time unprecedented, array of hominin craniofacial and dental form, much of which appears related to the elaboration of postcanine megadonty subsequent to *A. afarensis*. While the relatively primitive masticatory system of *A. afarensis* makes it a *plausible* ancestor for any or all of these younger taxa, neither sample size, nor anatomical representation, nor stratigraphic density of the fossil record makes defining lineages across the 3.0- to 2.5-Ma time period a meaningful exercise. Nevertheless, by 2.8 Ma or so, we can perceive the diverse products of what can be hypothesized as a series of speciation events that laid the groundwork for the evolutionary events of the late Pliocene.

Key references: Asfaw et al. 1999.

Australopithecus robustus (Broom 1938)

Known temporal distribution: ca. 1.5–2.0 Ma based on biochronologic correlation with radioisotopically calibrated east African sequences.

Known geographical distribution: Kromdraai, Swartkrans, Drimolen, South Africa.

Holotype: TM 1517 cranium, mandible, and purportedly associated talus from Kromdraai

Hypodigm: Approximately 250 specimens of jaws, teeth, crania, and postcranial elements from the Swartkrans cave (Brain 1993); a much smaller sample of teeth (approximately 30), in addition to the holotype, from Kromdraai (Thackeray et al. 2001); and more than 80 dentognathic specimens, including a cranium with associated mandible from Drimolen (Keyser 2000; Keyser et al. 2000).

Diagnostic morphology (Fig. 3) : Broom's (Broom and Schepers 1946) inference regarding the specific distinctiveness (from *A. africanus* sensu lato) of the Kromdraai skull and dentition was based on its disproportionately large postcanine dentition and unusual facial morphology, which features broad, anteriorly placed zygomatic bones and depressed infraorbital surfaces and nasal bridge between them (the so-called dished face). The large sample of teeth, jaws, and crania accumulated during postwar excavations at Swartkrans added significantly to the *A. robustus*

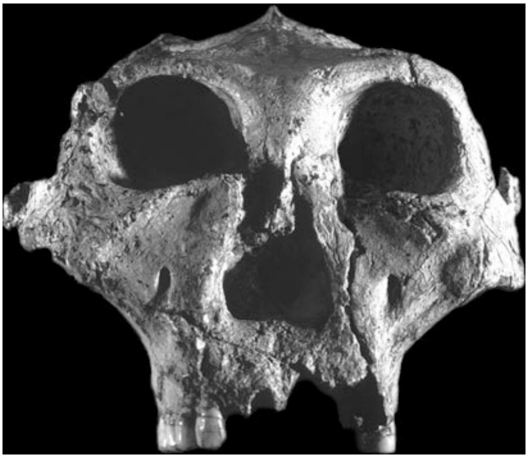

Fig. 3 Anterior view of Swartkrans *A. robustus* cranium SK 48 (Photo by W. Kimbel)

diagnostic profile, including buccolingually expanded and molarized premolars and lower deciduous first molars; premolar and molar crowns with convergent cusp apices and very thick enamel caps that wear to flat occlusal planes soon after eruption; mandibles with transversely thick and inflated bodies and vertically high rami; deep, posterosuperiorly sloping palatal roofs; a depressed posttoral frontal squama delimited by strongly incurving temporal lines ("frontal trigone"); and frequent frontoparietal sagittal crests. The large series of juvenile mandibles (with fully deciduous or mixed dentition) and a fragmentary, edentulous juvenile maxilla (SK 66), all from Swartkrans, demonstrate that many components of this pattern, especially postcanine megadontia and gnathic robusticity were manifested early in craniofacial ontogeny. Robinson (1953b) drew attention to the unusual nasal cavity configuration in *A. robustus*, which includes a smooth ("unstepped") transition from the subnasal surface to the nasal cavity floor, and a retracted position of the anterior nasal spine within the nasal cavity where it merges with the anterior insertion of the vomer (also observed in *A. boisei* and *A. aethiopicus*).

Rak's (1983) study of the australopith face identified a constellation of unique circumnasal (nasoalveolar gutter, maxillary fossula – the highly modified canine fossa, anterior pillar – less prominent than what is seen in *A. africanus*) and infraorbital traits (zygomaticomaxillary step, maxillary trigone) related to the posterior retraction of the palate and the anterior encroachment of the zygomatic bones (to originate above the premolars) on the midface. These antagonistic "shifts" lend the Swartkrans and Kromdraai crania their humanlike orthognathic appearance, and though the subnasal maxilla itself remained primitively prognathic, the facial aspect of the premaxillary suture fused prior to adulthood, again, as in humans.

Among the humanlike characteristics of the *A. robustus* type specimen that most impressed Broom (Broom and Schepers 1946) was the basal aspect of the temporal bone. The variably deep mandibular fossa with discrete articular eminence, small postglenoid process, vertically oriented, platelike tympanic element with prominent petrous crest and frequently well-developed vaginal process of the styloid, and the narrow or absent gap between the postglenoid process and tympanic are found with remarkable consistency in the now numerous cranial bases of *A. robustus* (e.g., SK 46, SK 47 [subadult], SK 48, SK 49, SK 52/SKW 18, SK 83, SKW 11, SKW 2581) and all converge on modern human morphology. Though elements of this pattern can be found in *A. africanus*, they are not presented in that taxon as a package. The single cranium of *A. aethiopicus* (KNM-WT 17000) presents notably less derived morphology in this area, sharing with *A. robustus* only the vertical tympanic with a strong petrous crest. The often dramatic lateral extension of the tympanic's inferior margin beyond the sagittal plane of porion and the coincident expansion of the diameter of the external auditory meatus are not seen in *A. afarensis*, *A. africanus*, or *A. aethiopicus*.

Discussion: The craniodental remains of *A. robustus* present a coherent and highly distinctive anatomical package across the three South African sites in which they are represented. Although a species-level distinction between the Kromdraai (*A. robustus*) and Swartkrans (*A. crassidens*) site samples has been proposed on the basis of metrical and morphological differences in the permanent and deciduous postcanine teeth – according to which the Kromdraai specimens appear less highly differentiated, and thus more similar to the teeth of *A. africanus* (Grine 1993) – reported variation within the Drimolen "robust" australopith sample spans the differences between the Kromdraai and Swartkrans dental collections (Keyser et al. 2000), making a site-based taxonomic split difficult to support.

With the proliferation of the east African hominin fossil record in the 1960s–1980s, there developed a tendency to see the South African australopiths as poised in morphological and adaptive transition between the generalized *A. afarensis* and the specialized *A. boisei*. Rak's (1983) morphocline of australopith craniofacial morphology was explicit in this regard, though when translated into a phylogenetic scenario, it allowed for cladogenesis between an *A. africanus* to *A. robustus* lineage and *A. boisei* on the basis of the overlap of the two "robust" species' temporal ranges. The recognition of the biological validity of *A. aethiopicus* rendered the *A. africanus* to *A. robustus* lineage unlikely due to the extensive character reversal it would entail given the former species' derived zygomaticomaxillary and postcanine dental morphology. While a polyphyletic origin for the "robust" morphology via separate eastern (*A. aethiopicus* to *A. boisei*) and southern (*A. africanus* to *A. robustus*) lineages is plausible, this scheme does not gain support from phylogenetic analyses of craniofacial characters, which strongly back a monophyletic "robust" clade to the exclusion of *A. africanus*. Thus, the potential for a single australopith species lineage in southern Africa is weak (and notwithstanding the poor chronological resolution within these hominin-bearing deposits).

Key references: Broom and Schepers 1946; Broom and Robinson 1952; Robinson 1956; Rak 1983; Grine 1988, 1993; Grine and Strait, 1994; Keyser 2000; Keyser et al. 2000.

***Australopithecus boisei* (Leakey 1959)**

Known temporal distribution: ca. 2.4–1.4 Ma, based on radioisotopic dating and tephrostratigraphy.

Known geographical distribution: Olduvai Gorge (Beds I and II), Tanzania; Peninj (Humbu Formation), Tanzania; Omo River basin (Shungura Formation, Member G), Ethiopia; Konso, Ethiopia; Koobi Fora (Koobi Fora Formation); West Turkana (Nachukui Formation), Kenya; Chesowanja, Kenya

Holotype: OH 5, cranium with full dentition, from Bed I, Olduvai Gorge

Hypodigm: Aside from the holotype, isolated teeth from Beds I and II, Olduvai Gorge (Tobias 1967); several mandibles, a partial cranium, and many isolated teeth from the Omo River basin (Shungura Formation, Member G); six complete or partial crania, more than 20 mandibles, and several maxillae with and without teeth from Koobi Fora (Wood 1991), a partial subadult cranium from West Turkana (Leakey and Walker 1988), two partial crania from Chesowanja (Carney et al. 1971; Gowlett et al. 1981), and a mandible with full dentition from Peninj (Leakey and Leakey 1964); a partial cranium with associated mandible, plus isolated teeth and jaw and cranial fragments from Konso, Ethiopia (Suwa et al. 1997).

Diagnostic morphology (Figs. 4 and 5): *A. boisei* presents one of the most easily recognized morphological patterns in the early hominin fossil record, due chiefly to uniquely derived states for many of its skull and dental characters. Tobias's (1967, pp. 232–233) study of the holotype cranium supported the specific distinctiveness (relative to *A. robustus*) of the Olduvai hominin, citing, among other features, the absolutely larger (especially broader) postcanine teeth, greater disproportion between the postcanine and anterior dentitions, stronger supraorbital torus, shorter foramen magnum, absence of "even the slightest trace of a canine fossa," structure of the zygomatic region, anterior flexion of the palate, and "evidences of marked

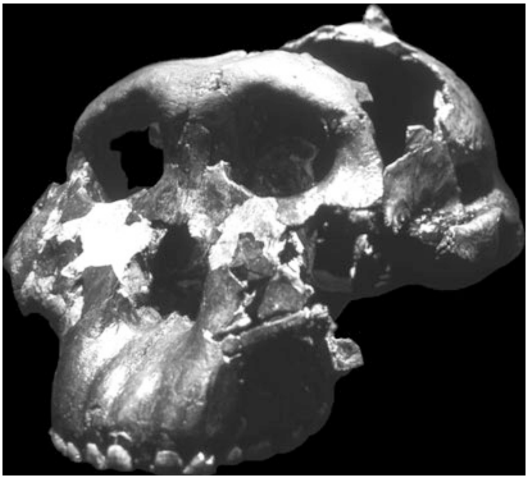

Fig. 4 Three-quarters view of the reconstructed cranium of *A. boisei* holotype specimen OH 5 (Photo by D. Johanson)

Fig. 5 Palate and maxillary dentition of *A. boisei* specimen OH 5 (Photo by D. Johanson)

parietal lobe and cerebellar expansion." Except for the foramen magnum and inference of brain expansion, these distinctions reside in the dentognathic complex, and it is here that most subsequent writing on the diagnostic morphology of *A. boisei* has been focused. In general terms, *A. boisei* has often been characterized as "hyper-robust," essentially an extreme version of *A. robustus*. Indeed, much of the specific craniofacial morphologies of *A. boisei* identified by Rak (1983), such as the elevated infraorbital "visor" (and its effects on the zygomatic arch), the (at least occasionally) inferolaterally sloping and "twisted" supraorbital bars, and the absence of an anterior pillar and maxillary fossula, were interpreted by him as signaling culminations of adaptive trends associated with masticatory specialization (retraction of the palate and advancement of the zygomatic region) that had already begun in *A. africanus*. The massiveness of *A. boisei* mandibular corpora (notwithstanding taphonomic effects on preserved dimensions among some of the largest of these; Silverman et al. 2001) surpasses even the most heavily built *A. robustus* jaws so far known (e.g., KNM-ER 3230 or KGA10-525 versus SK 12). There is, however, a high degree of variation in corpus size (but less so in corpus shape) among the mandibles of both species.

Discoveries made since OH 5 confirm that the postcanine dentition of *A. boisei* is substantially enlarged relative to that of *A. robustus* (White et al. 1981; Grine 1993). The mandibular P4 is particularly diagnostic of *A. boisei*, not only due to its larger size relative to the molars but also to its derived talonid expansion and molarization (Suwa 1988), also a tendency, though not as consistent, of the lower molars (Suwa et al. 1996). Whether measured as lower canine breadth or lower central incisor-canine alveolar length, the *A. boisei* anterior dentition is smaller relative to the cheek teeth than in *A. robustus* (Suwa et al. 1996). (Upper teeth of *A. boisei* remain poorly known relative to the lower, a phenomenon associated with the differential taphonomic attributes of the mandible versus the maxilla.)

The cranial base of *A. boisei* has received less attention than the dentognathic part of the skull but the morphology here is no less specialized (Kimbel et al. 2004). In lateral aspect, the mastoid process appears as an equilateral triangle, with an extensive, swollen lateral face that is sharply delimited from the posterior face, mostly hidden in this view, and the mastoid tip lies approximately midway between the projected horizontal line spanning asterion to porion. This configuration is unmatched in the large majority of other *Australopithecus* crania, in which the mastoid is dominated by an extensive posterolateral face with a long, straight posterior margin that converges with a shorter anterior margin to position the tip much closer to porion than to asterion. This is the generalized pattern common to the great apes, *A. afarensis* and *A. africanus*. Some *A. robustus* specimens approach the *A. boisei* anatomy (i.e., SKW 11), though most are more generalized, as is that of the *A. aethiopicus* cranium KNM-WT 17000.

The region around the mandibular fossa is also unique in *A. boisei* among australopith species. The articular fossa is very deep, with the highest point on the ceiling reaching above the Frankfurt plane, and the long steep articular eminence terminates at the posterior edge of the temporal foramen. The preglenoid plane is usually mediolaterally restricted. The articular eminence twists about its long axis such that medially it faces posteriorly, and the pyramidal entoglenoid process likewise points backward to create a flat "medial glenoid plane" at the medial end of the eminence. The platelike tympanic element is often flattened superiorly and inclined posteriorly, giving the external auditory meatus an oval shape with a diagonal long axis. In some specimens (e.g., KNM-ER 406, OH 5), this inclined tympanic forms more of the ceiling of the mandibular fossa than its posterior wall, and the petrous crest blends with the anterior face of the mastoid process, resulting in obliteration of the tympanomastoid groove. In all of these respects, the cranial bases of *A. robustus* and *A. aethiopicus* are more generalized.

Discussion: There is statistical backing for a trend (though not necessarily a gradual one) toward larger postcanine tooth size in *A. boisei* (sensu stricto) between 2.0 and 1.4 Ma (Wood et al. 1994; Lockwood et al. 2000). There is no evidence of change in mandibular corpus size over this interval. Prior to 2.0 Ma, the east African "robust" australopith fossil record is not well documented, but evidence for a species lineage that extends back in time from *A. boisei* focuses on specimens that lack the full suite of derived craniodental characters enumerated above. "Robust" australopith dental remains, especially the lower premolars, from Members D–F of the Shungura Formation (ca. 2.5–2.3 Ma) are less derived than those of post-2.0 Ma *A. boisei* (Suwa et al. 1996), as reviewed above (see discussion of *A. aethiopicus*). Cranial specimens of the "robust" morphotype from the pre-2.0-Ma period are rare, but the lower Member G partial cranium Omo 323-1976-896 (ca. 2.1 Ma), attributed by Alemseged et al. (2002) to *A. boisei*, lacks a number of the cranial autapomorphies that characterize the post-2.0-Ma skulls of this species, including mastoid, tympanic, articular eminence, preglenoid, and entoglenoid characteristics (Kimbel et al. 2004; see also Alemseged et al. 2002). In these respects, the Omo cranium resembles the more generalized *A. robustus*, yet it is less similar to *A. aethiopicus* – the Omo specimen has a deeper mandibular fossa and probably, based on the preserved maxillary fragment, less midfacial prognathism compared to KNM-WT 17000 (2.5 Ma) – which implies an immediate predecessor of *A. boisei* in eastern Africa that was cranially more like southern African *A. robustus* than like eastern African *A. aethiopicus*. Suwa (1988; Suwa et al. 1996) reported a mix of derived and generalized "robust" australopith postcanine crown morphologies in Member G of the Shungura Formation (ca. 2.3–2.0 Ma), which is consistent with the relatively generalized anatomy of the Omo 323 cranium at ca. 2.1 Ma. This evidence has been used to support an anagenetic derivation of *A. boisei* from a chain of progressively less derived "robust" populations leading back to *A. aethiopicus* at ca. 2.5 Ma or older (Kimbel et al. 1988; Leakey and Walker 1988; Suwa et al. 1996; Alemseged et al. 2002). If true, this would argue for the existence of a single-species lineage of over 1-Myr duration, which is about the documented span of the hypothesized *A. anamensis* to *A. afarensis* species lineage of the earlier Pliocene (Kimbel et al. 2006). However, given the demonstrated morphological links of the eastern African "robust" specimens between 2.0 and 2.3 Ma to *A. robustus*, and the report of otherwise unique *A. robustus* characters within a diagnostic *A. boisei* morphological milieu in the late (1.4 Ma) partial skull from Konso, Ethiopia (Suwa et al. 1997), reconstructing a direct phyletic link between *A. aethiopicus* and *A. boisei* would require positing a cladogenetic event giving rise to a southern African "robust" branch within the 2.3–2.0-Ma interval. Thus, an unbroken, anagenetically evolving "robust" australopith species lineage in the eastern African middle-late Pliocene is unlikely.

Key references: Tobias 1967; Grine 1988; Wood 1991; Wood et al. 1994; Suwa et al. 1996, 1997; Alemseged et al. 2002; Kimbel et al. 2004; Wood and Constantino 2007.

Conclusion

Given a strict evolutionary species definition, nominal taxonomic diversity and species-lineage diversity do not necessarily map onto one another in the fossil record. Species lineages entail statements of ancestry and descent that depend on the consistency of phylogenetic and stratophenetic data. The requirements for identifying species lineages in the fossil record are severe and rarely met in the early hominin record, most often owing to small sample size, underrepresented character data, nonrepresentation of rare or short-lived taxa, poor chronological resolution, gaps in the time-stratigraphic framework, or some combination of these factors. Because hypotheses concerning the "bushiness" of the hominin phylogenetic tree depend on the identification of lineages, not phenetically based "paleospecies," confidence with respect to this issue is not justified for the majority of the hominin fossil record.

The fossil record of australopith evolution in eastern Africa offers two cases in which an approach to this question can be attempted. In one, the evidence, though still imperfect, is consistent with the evolution of *A. anamensis* into *A. afarensis* via anagenesis (i.e., without an increase in lineage diversity). The other, the evolution of *A. boisei*, is almost certain to have entailed a speciation event that gave rise to southern African clade (represented by *A. robustus*) subsequent to the appearance of *A. aethiopicus*. The late Pliocene time period in which the latter events transpired (ca. 2.8–2.3 Ma) was one of substantial morphological diversity, high nominal taxonomic diversity, and high probability of synchronicity among known fossil samples. Although it is not possible to connect these australopith taxa (*A. aethiopicus, A. africanus, A. garhi*) to particular descendants due to the aforementioned defects in the database – and indeed, it is not unlikely that some or all of these species are terminal taxa – once it is better known, this period will most likely be seen to have witnessed a previously (and subsequently) unmatched degree of lineage proliferation compared to other parts of the human evolutionary record. The challenge to paleoanthropologists is to devote resources to improving this part of the fossil record and then to create testable phylogenetic and adaptive hypotheses to explain it.

Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ The Miocene Hominoids and the Earliest Putative Hominids

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Defining the Genus *Homo*

Mark Collard and Bernard Wood

Contents

Abstract

The definition of the genus *Homo* is an important but under-researched topic. In this chapter we show that interpretations of *Homo* have changed greatly over the last 150 years as a result of the incorporation of new fossil species, the discovery of fossil evidence that changed our perceptions of its component species, and reassessments of the functional capabilities of species previously allocated to *Homo*. We also show that these changes have been made in an ad hoc fashion. Criteria for recognizing fossil specimens of *Homo* have been outlined on a

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M. Collard (✉)
Human Evolutionary Studies Program and Department of Archaeology, Simon Fraser University, Burnaby, BC, Canada

Department of Archaeology, University of Aberdeen, Aberdeen, UK
e-mail: mcollard@sfu.ca

B. Wood
Center for the Advanced Study of Human Paleobiology, Department of Anthropology, George Washington University, Washington, DC, USA

Human Origins Program, Smithsonian Institution, Washington, DC, USA
e-mail: bernardawood@gmail.com

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number of occasions, but these criteria have generally not been explicitly derived from a genus concept. Rather, the course of action followed by most researchers has been to assign new specimens to *Homo* on the basis of a subset of the diagnostic traits that are considered to be key, and to then redefine the other traits of the genus in the light of the morphological and functional attributes of the new specimens. With a view to moving beyond this approach, in the next section of the chapter we outline six competing proposals for how genera should be defined, and consider their impact on the species assigned to the genus *Homo*. Subsequently, we consider the pros and cons of the six genus concepts. We argue that three of them are impractical and/or internally inconsistent, and that three are useful. We go on to suggest that, while there is little to choose between the latter three concepts on theoretical grounds, the one put forward by Wood and Collard (Science 284: 65–71, 1999) has practical advantages. In the last part of the chapter, we update Wood and Collard's review of genus *Homo* in the light of research published since their study appeared. We find that, on balance, the available evidence still supports their suggestion that *Homo* should be reconfigured such that it includes *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens* but excludes *H. habilis* and *H. rudolfensis*. We also find that the proposed inclusion of the collection of Late Pleistocene specimens from the site of Liang Bua, Flores, in the genus *Homo* as a new species, *H. floresiensis*, is not compatible with Wood and Collard's definition of the genus *Homo*.

Introduction

It is obvious – indeed it is so obvious that it bears repeating – that an understanding of the evolution of genus *Homo* depends, to a considerable extent, on the proper definition of the classificatory categories "genus" and "species," and the correct evaluation of the taxa that are assigned to these categories. In recent years, the species category has received considerable attention from paleoanthropologists (e.g., Tattersall 1986; Turner and Chamberlain 1989; Kimbel and Martin 1993) and there has been a taxonomic rationalization of material previously grouped as "early *Homo*" and "archaic *Homo sapiens*" into reasonably robust species groups (e.g., Tattersall 1986, 1992; Lieberman et al. 1988; Wood 1991, 1992; Wood et al. 1991; Rightmire 1993, 1996, 1998). In contrast, both the definition of the genus category and the demarcation of the genus *Homo* remain contentious. In this chapter, we outline the main events that have taken place in the taxonomic history of the genus *Homo*. We then evaluate several recent proposals to amend the criteria that are used to assign species to genus *Homo*, and show that the criteria we outlined in the late 1990s (Wood and Collard 1999) are the least problematic. Lastly, we discuss the effect of recent work on the main conclusion we reached when we applied our criteria to the species then assigned to genus *Homo*, namely that *Homo habilis* and *Homo rudolfensis* should be assigned to a different genus or pair of genera (Wood and Collard 1999).

Changing Interpretations of Genus *Homo*

The genus *Homo* was established by Carolus Linnaeus in the 10th edition of his *Systema Naturae*, published in 1758. As conceived by Linnaeus, the genus incorporated two species. The name *Homo sapiens* was attached to what Linnaeus described as the more diurnal of the two species. Within *H. sapiens*, Linnaeus recognized six groups. Four of these are geographical variants drawn from the four continents known to Linnaeus, namely Africa, America, Asia and Europe. The other two groups, which Linnaeus called "wild men" and "monstrous men" respectively, are of historical rather than biological interest. A similar conclusion probably also applies to Linnaeus' second species of *Homo*, *Homo sylvestris*, also called *Homo troglodytes* or *Homo nocturnes*, which he suggested is a nocturnal cave-dwelling form of human from Java. *H. sylvestris* is widely regarded as mythical, although the recent discovery of *Homo floresiensis* (see below) raises the possibility that it may have had some basis in fact.

The first fossil species was assigned to *Homo* in 1864. In this year the Irish geologist William King referred a partial skeleton that had been recovered in 1856 from the Feldhofer cave in the Neander Valley in Germany to *Homo neanderthalensis*. King considered naming a new genus for the Feldhofer skeleton, but eventually decided that it was sufficiently similar to *H. sapiens* to warrant its inclusion within *Homo*. In the same year George Busk reported to the British Association for the Advancement of Science what we now know to be a Neanderthal cranium from Gibraltar (Busk 1865). Although Busk acknowledged the strength of the resemblance between the Gibraltar cranium and the one from the Neanderthal Cave, he judged the former to belong to *H. sapiens*, albeit a member of the species that was more similar to living Tasmanians and Australians than to contemporary Europeans. The inclusion of the Neanderthal skeleton within *Homo* expanded the ranges of both the cranial and postcranial morphology of the genus. The morphology of the type specimen, together with evidence gleaned from discoveries made prior to 1856 and thereafter in Western Eurasia, show that Neanderthal crania differ from those of *H. sapiens* in several respects. Typically, they have discrete and rounded supraorbital ridges, faces that project anteriorly in the midline, laterally-projecting and rounded parietal bones, a rounded, posteriorly projecting, occipital bone, a derived nasal morphology (Schwartz and Tattersall 1996; but see Franciscus 1999), large incisor teeth, and postcanine teeth with large root canals. Their brains were as large, if not larger, in absolute terms than the brains of modern humans. Postcranial peculiarities of the Neanderthals include limb bones with stout shafts and relatively large joint surfaces, especially well-marked areas for the attachment of a muscle that helps to control movement at the shoulder, and an elongated pubic ramus of the pelvis (Pearson 2000).

The morphological variability of genus *Homo* was further extended between 1908 and 1933 by the addition of a group of specimens that was initially referred to as "archaic *Homo sapiens*" but is now more often called *Homo heidelbergensis* (Tattersall 1986, 1992; Rightmire 1996, 1998). The type specimen of *H. heidelbergensis* is a mandible that was found in 1907 during excavations to extract sand from a quarry at Mauer, near Heidelberg, Germany (Schoetensack 1908). The next evidence within Europe came in 1933 from a gravel-pit at Steinheim in Germany, but in the meantime evidence had also been found at the site of Kabwe in what was then Rhodesia (Woodward 1921). The brain cases of *H. heidelbergensis* are often, but not always, smaller than those of modern humans (e.g., Steinheim), but they are always more robustly built, with large rounded ridges above the orbits and a thickened occipital region. The Mauer mandible has no chin, and the corpus is substantially larger than those of modern Europeans. Postcranially, the shapes of the limb bones are much like those of *H. sapiens*, except that the shafts of the long bones are generally thicker, with higher robusticity indices. Schoetensack's (1908) decision to refer the Mauer mandible to *H. heidelbergensis* altered the interpretation of *Homo* in that it added a taxon with a mandible more primitive than those of either *H. sapiens* or *H. neanderthalensis*. The subsequent addition of the Kabwe specimen to *Homo* meant that the genus now included a species with a more heavily built cranium than either *H. sapiens* or *H. neanderthalensis*.

The range of morphology within *Homo* was widened again in 1940 when Franz Weidenreich formally proposed that two existing hypodigms, *Pithecanthropus erectus* and *Sinanthropus pekinensis*, should be merged into a single species and transferred to *Homo* as *Homo erectus* (Weidenreich 1940). Subsequently the hypodigms of *Meganthropus* (Mayr 1944, p. 14; Le Gros Clark 1955, pp. 86–87), *Atlanthropus* (Le Gros Clark 1964, p. 112) and *Telanthropus* (Robinson 1961; Howell 1978, p. 198) were also sunk into *H. erectus*. Compared with *H. sapiens*, *H. neanderthalensis* and *H. heidelbergensis*, most fossils attributed to *H. erectus* have a smaller neurocranium, a lower vault, a broader base relative to the vault, and more complex premolar roots. They also have a substantial and essentially continuous torus above the orbits, behind which is a sulcus. There is usually a sagittal torus, and also an angular torus that runs towards the mastoid process. The occipital region is sharply angulated, with a well-marked supratoral sulcus, and the inner and outer tables of the vault are thickened. Despite the relatively large numbers of crania that had been recovered from Java, China and elsewhere, relatively little was known about the postcranial morphology of what was to become *H. erectus*. Discoveries from East African sites provided crucial evidence in the form of a from pelvis and femur Olduvai Gorge (OH 28), two fragmentary partial skeletons from and a pelvis East Turkana (e.g., KNM-ER 803, 1800 and 3228), and the unusually well-preserved skeleton from West Turkana (KNM-WT 15000). The cortical bone of the postcranial skeleton is generally thick. The long bones are robust, and the shafts of the femur and the tibia are flattened from front to back relative to those of other *Homo* species; these conditions are referred to as platymeria and platycnemia, respectively. However, all the postcranial elements are consistent with a habitually upright posture and long-range bipedalism.

In 1964, Louis Leakey, Phillip Tobias and John Napier announced the discovery at Olduvai Gorge of specimens that they believed belonged to a previously unknown species of *Homo*, which they called *Homo habilis* (Leakey et al. 1964). These specimens (OH, 4, 6, 7, 8, 13, 14 and 16) were found between 1959–when a new genus and species, *Zinjanthropus boisei*, had been created for the famous "Nutcracker Man" cranium, OH 5–and 1963. The type specimen of *H. habilis*, OH 7, recovered in 1960, consists of substantial parts of both parietal bones, much of a mandible and several hand bones of a juvenile skeleton. In the next three years further evidence of a "non-robust" fossil hominin was unearthed in Bed I of Olduvai Gorge (OH 8 – an adult foot; OH 14 – juvenile cranial fragments, and OH 16 – the fragmented cranial vault and maxillary dentition of a young adult) as well as in Bed II (OH 13 – the incomplete skull of an adolescent). The inclusion of this group of specimens in *Homo* substantially widened the range of morphology within the genus, and meant that Le Gros Clark's 1955 diagnosis needed to be amended. In particular, in order to accommodate *H. habilis* in the genus, Leakey et al. (1964) reduced the lower end of the range of brain size to 600 cm^3. They claimed that other criteria, such as dexterity, an erect posture and a bipedal gait, did not need to be changed because their interpretation of the functional capabilities of the *H. habilis* remains from Olduvai was such that the type specimen and the paratypes complied with these functional criteria (Leakey et al. 1964). Ultimately fresh evidence, and the reinterpretation of existing evidence, has led others to offer rather different functional assessments of the same material (see below).

The systematic interpretation of *Homo* was further complicated in 1972 by Richard Leakey and colleagues' discovery of KNM-ER 1470. Recovered from the Upper Burgi Member of the Koobi Fora Formation, KNM-ER 1470 is now reliably dated to between 1.945 ± 0.004 and 2.058 ± 0.034 Ma (Joordens et al. 2013). Morphologically, it presents a unique mixture of a relatively large, *Homo*-like neurocranium and a large, broad *Paranthropus*-like face. The presence of these two morphologies in the same cranium posed a difficulty for researchers. Which was the homoplasy – the large brain or the large face? Alone among the early commentators, Alan Walker (1976) cautioned that KNM-ER 1470 may represent a large-brained australopith. Most researchers chose the face as the site of homoplasy and argued that the large neurocranium allied the specimen with *Homo* (e.g., Leakey 1973; Rak 1987; Bilsborough and Wood 1988). As a consequence, *Homo* subsumed a substantially wider range of facial morphology than it did prior to the discovery of KNM-ER 1470 (Wood 1991).

In due course, additional specimens from Koobi Fora (e.g., KNM-ER 1590, 1802, 1813, 3732, 60000, 62000, 62003) (Wood 1991; Leakey et al. 2012), and Olduvai (e.g., OH 62, 65) (Johanson et al. 1987; Bermudez de Castro et al. 2003; Clarke 2012) were added to the early *Homo* hypodigm, as was fossil evidence from Members G and H of the Shungura Formation (Howell and Coppens 1976; Boaz and Howell 1977; Coppens 1980), A.L. 666-1 from Hadar (Kimbel et al. 1997), a temporal bone from the Chemeron Formation (Hill et al. 1992), a mandible from Uraha in Malawi (Bromage et al. 1995), and an isolated tooth from the Nachukui Formation, West Turkana (Prat et al. 2005). Fossils from southern African sites, Member 5 at Sterkfontein (Hughes and Tobias 1977; Clarke 1985), and Member 1 at Swartkrans (Clarke and Howell 1972; Grine and Strait 1994; Grine et al. 1993, 1996) and Drimolen (Curnoe and Tobias 2006), were also added. This additional material subsumes a wide range of cranial morphology. For example, the endocranial volumes of the specimens range from just less than 500 cm^3 to around 850 cm^3. The mandibles also vary in size, with those from the larger individuals having robust bodies and premolar teeth with complex crowns and roots. The discovery of OH 62 was particularly significant with regard to the postcranial anatomy of *H. habilis*. Although the preservation of this specimen is poor, its skull is sufficiently well preserved to be confident that it does not belong to *Paranthropus boisei*. Thus, unless it is the first evidence from Bed I of a novel taxon, then OH 62 must belong to *H. habilis*, the only other hominin species known from that time range at Olduvai Gorge. Although several isolated postcranial specimens from Bed I had been attributed to *H. habilis* (Leakey et al. 1964), it was subsequently pointed out that it is at least equally likely that this postcranial evidence belongs to *P. boisei* (Wood 1974). The discovery of OH 62 provided the first unequivocal postcranial evidence of *H. habilis*. It is significant therefore that OH 62 has been interpreted as having limb proportions that are at least as ape-like as those of individuals attributed to *Australopithecus afarensis* (Johanson et al. 1987; Hartwig-Scherer and Martin 1991; Richmond et al. 2002).

The morphological limits of genus *Homo* were expanded once again in 2004 with the announcement of the species *Homo floresiensis* (Brown et al. 2004). The specimens initially attributed to this species were recovered from deposits in the Liang Bua cave on the Indonesian island of Flores, and are dated to between approximately 74,000 and 18,000 years ago (Brown et al. 2004; Morwood et al. 2004), but they may be closer to 100 Ka. They include a well-preserved skull and partial skeleton of an adult female as well as several more fragmentary specimens (Brown et al. 2004). Since 2004 additional upper limb evidence of the type specimen, LB1, has been recovered, together with a second adult mandible (LB6), and postcranial remains belonging to other individuals (LB4, 5, 7, 8-9) (Morwood, et al. 2005). *H. floresiensis* is a particularly significant addition to *Homo* because of its brain size. The endocranial volume of the partial associated female skeleton, LB1, was initially reported to be 380 cm^3 (Brown et al. 2004). Subsequently, Falk et al. (2005) increased this figure to 417 cm^3. Even at 417 cm^3, the endocranial volume of *H. floresiensis* is considerably smaller than those of the other species assigned to *Homo*. Among the latter, *Homo habilis*, *Homo rudolfensis*, and *Homo erectus* (including *Homo ergaster*) have the smallest endocranial volumes. Adult endocranial volume in *H. habilis* presently ranges between 509 and 674 cm^3 (Tobias 1991; Kappelman 1996). Only one of the specimens assigned to *H. rudolfensis* is sufficiently complete to provide an adult endocranial volume for this species. The specimen in question, KNM-ER 1470, is estimated to have an endocranial volume of 752 cm^3 (Kappelman 1996). Currently the upper limit of adult endocranial volume in *H. erectus* is 1,251 cm^3 (Rightmire 2004); the lower limit is either 775 cm^3 or ~600 cm^3 depending on the taxonomic status of the D2700 cranium from Dmanisi (Vekua et al. 2002; Rightmire 2004). Thus, the assignment of the Late Pleistocene Liang Bua specimens to *Homo* greatly increases brain size variation in the genus. The body of *H. floresiensis* has been suggested to be small compared to other species of *Homo* (Lahr and Foley 2004). However, the stature estimates of 106 cm for LB1 (Brown et al. 2004) and 109 cm for LB8

(Morwood et al. 2005) are only slightly smaller than McHenry's (1991) stature estimate of 118 cm for the *H. habilis* partial skeleton OH 62.

Interpretations of *Homo* have also changed as a result of researchers reassessing the functional implications of the postcranial remains from Olduvai Gorge that are conventionally attributed to *H. habilis*. The type and paratypes of *H. habilis* include fossil evidence from both the forelimb (OH 7) and the hindlimb (OH 8, 10 and 35) (some have argued that OH 8 and 35 are from the same individual [Susman and Stern 1982], but an analysis of the shapes of the reciprocal joint surfaces suggests otherwise [Wood et al. 1998]). The initial assessment of the functional implications of the evidence from the leg and foot stressed the ways in which the Olduvai material resembled *H. sapiens* (Napier 1964). However, the authors of papers in which these specimens have been considered in more detail have been more cautious. For example, they have stressed that the knee was imperfectly adapted to bipedalism (Davis 1964), and that the foot may not have been from an individual capable of modern human-like striding bipedalism (Day and Napier 1964). Functional morphological studies of the OH 8 foot have also stressed its potential for climbing, and its retention of several of the features seen in living non-human primates (Lewis 1983, 1989; Susman and Stern 1982; Kidd et al. 1996; Gebo and Schwartz 2006). Researchers have suggested that, while OH 8 possesses the articular mechanisms that convert the foot into a rigid lever during the support phase of walking (Lewis 1989), it lacks some of the functional elements that are present in *H. sapiens* such as the lateral deviation of the heel and the propulsive great toe (Lewis 1972). Similarly, considerations of the OH 7 hand have suggested that earlier functional interpretations may need to be revised in the light of evidence that it displays a mosaic of features, ranging from ape-like phalanges and carpus to a thumb that some have interpreted as compatible with pulp-to-pulp opposition (Susman and Creel 1979; Marzke 1997; Susman 1998).

Today, as a result of the developments outlined above, the genus *Homo* subsumes considerably more variation than it did when it was first established 250 years ago. This variation is particularly obvious in relation to cranial capacity. The adult *Homo* specimen with the largest recorded cranial capacity is the Neanderthal skeleton Amud 1 at an estimated 1,750 cm^3. At the other end of the spectrum lies the type specimen of *H. floresiensis*, Liang Bua 1, with a cranial capacity of 417 cm^3. To put this in perspective, at 1750 cm^3 the braincase of Amud 1 is almost 100 cm^3 larger than the largest *H. sapiens* specimen included in one of the most comprehensive studies of human brain size published to date (Beals et al. 1984), while the braincase of Liang Bua 1 is slightly smaller than that of an average-sized adult male chimpanzee (Kappelman 1996). Variability is also conspicuous in relation to masticatory morphology. For example, the lower first molars of the *Homo* species with the largest M_1s, *H. rudolfensis*, are 32 % larger mesiodistally than those of the *Homo* species with the smallest M_1s, *H. neanderthalensis* (Wood and Collard 1999). Likewise, average mandibular corpus width at M_1 in *H. rudolfensis*, the *Homo* species with the widest mandibular corpus, is 77 % greater than it is in *H. sapiens*, the *Homo* species with the narrowest mandibular corpus (Wood and Collard 1999). Noteworthy variability in locomotor strategies exists as well. Most of the fossil species assigned to *Homo* are interpreted as having been obligate bipeds like *H. sapiens*. However, as noted earlier, in recent years the postcranial specimens assigned to *H. habilis* have come to be viewed by most researchers as being consistent with bipedalism combined with an ability to climb proficiently (McHenry and Coffing 2000; Wood and Richmond 2000; Ruff 2009). Thus, there would seem to be at least two distinct modes of locomotion represented within *Homo*.

Is Genus *Homo* a "Good" Genus?

In view of the conspicuous variation incorporated within the hypodigm of *Homo*, it seems reasonable to ask whether it is a "good" genus as it is currently construed. Needless to say, in order to determine whether or not *Homo* is a "good" genus there must first be agreement about what it is that genera represent.

Surprisingly, the genus concept has received relatively little attention from taxonomists. It certainly has received much less consideration than the species concept even though as Simpson (1963, p. 199) notes "it frequently appears that the genus is a more usable and reliable unit for classification than the species." In the paleoanthropological literature, discussion of the genus as a concept has been very limited indeed. Criteria for recognizing fossil specimens of *Homo*, *Australopithecus* and other hominin genera have been outlined on a number of occasions (e.g., Le Gros Clark 1955; Howell 1978). But these criteria have generally not been explicitly derived from a genus concept. Rather, the course of action followed by most researchers appears to have been to assign new specimens to a fossil hominin genus on the basis of a subset of the diagnostic traits that the researchers in question deem to be key, and to then redefine the other traits of the genus in the light of the morphological and functional attributes of the new specimens. This is seen most clearly in relation to Leakey, Tobias and Napier's (1964) proposal to recognize *H. habilis*. As noted earlier, Leakey et al. (1964) assigned the *habilis* specimens from Olduvai Gorge to *Homo* on the grounds that, according to their interpretation of the available postcranial evidence, *H. habilis* stood upright and moved around using a bipedal gait, and was capable of modern human-like dexterity. They then amended the diagnosis of *Homo* presented by Le Gros Clark (1955) to take into account the 638–674 cm^3 brains of the Olduvai specimens. At no point in their paper do Leakey et al. (1964) discuss the pros and cons of assigning the Olduvai *H. habilis* specimens to *Homo* in terms of the genus as a concept.

If we wish to move beyond this ad hoc approach to assigning fossil hominin specimens to genera, what options are available? Currently, there are six competing proposals for how genera should be defined. We present them in chronological order of the main publication associated with each proposal. The first is associated with Ernst Mayr and the evolutionary systematic school of taxonomy. Mayr (1950, p. 110) suggested that "a genus consists of one species, or a group of species of common ancestry, which differ in a pronounced manner from other groups of species and are separated from them by a decided morphological gap." He went on to state that the genus "has a very distinct biological meaning. Species that are united in a given genus occupy an ecological situation which is different from that occupied by the species of another genus, or, to use the terminology of Sewall Wright, they occupy a different adaptive plateau" (Mayr 1950, p. 110). Thus, according to Mayr, a genus is a group of species of common ancestry that is adaptively both homogeneous and distinctive. Mayr et al. (1953, p. 50) acknowledged the phylogenetic and functional evidence may be in conflict if "unrelated species acquire a superficial similarity owing to parallel adaptations to similar environments," and in such cases they recommended that the phylogenetic evidence should be given precedence. However, it is implicit in Mayr's (1950) definition that "common ancestry" subsumes both monophyletic and paraphyletic groups.

The second concept of the genus is associated with Willi Hennig and the phylogenetic systematic or cladistic school of taxonomy. In his 1966 volume "Phylogenetic Systematics," Hennig outlined not only what has come to be known as the cladistic method of phylogenetic reconstruction, but also an approach to biological classification. With regard to the latter, Hennig (1966) suggested that only monophyletic groups should be accepted as valid taxa, and that the ranks assigned to taxa should be based on their time of origin so that taxa arising at the same time are assigned the same rank. Hennig (1966) recognized that strict application of the time of origin criterion for delineating ranks is impractical. This is because it would involve massive reorganization of current classifications of the living world, with some groups being lumped to a much greater extent and others being split much more finely. For example, as Hennig (1966) noted, if the time of origin criterion were to be applied strictly, then the first appearance date of Mammalia is such that the class would have to be downgraded to an order, and the orders that are assigned to it, such as Primates, would have to be downgraded to tribes. Conversely, the first appearance dates of some ostracod genera are such that they would have to be elevated to the class rank. Accordingly, Hennig proposed a compromise in which different time scales are employed for different animal groups, with the time scales being selected with a view to minimizing the number of changes in rank of subgroups.

The third genus concept focuses on hybridizability as the criterion for grouping species into genera. Although it has not been widely used by systematists to date, the origins of the concept can be traced back at least as far as the middle of the nineteenth century. Flourens (1856), for example, argued that two species whose members are able to produce hybrids, such as horses and donkeys, and jackals and dogs, should be placed in the same genus. More recently, the concept has been discussed by Hubbs and Drewry (1959), Van Gelder (1977, 1978), and Dubois (1988). The most comprehensive exposition of the hybridizability-based genus concept published to date is to be found in Dubois (1988). According to this author, when two species are able to produce viable adult hybrids both species should be included in the same genus. This is the case, Dubois (1988) suggested, regardless of whether the hybrids are fertile or infertile. If the two species in question had previously been attributed to distinct genera then they should be merged together even if other criteria for separating them are valid. In other words, Dubois (1988) argued that the ability to give birth to viable adult hybrids should be the primary criterion for grouping species into genera. Dubois (1988) stressed two additional points. One is that hybridization need not take place only in the wild to be admissible as evidence of the congeneric status of two species; the results of experimental studies are also acceptable. The other point he emphasized is that the criterion of hybridizability must only be used to group species together. A negative result – i.e., one where hybridization does not occur or where the hybrid is not viable – cannot be used to place two species in different genera.

The fourth genus concept was proposed by Wood and Collard (1999). These authors suggested that a genus should be defined as a species or monophylum whose members occupy a single adaptive zone. This definition, which is a revised version of Mayr's (1950) concept, differs from the latter in that it excludes paraphyletic taxa. It also differs from Mayr's (1950) concept in that it does not require the adaptive zone to be unique or distinct (*contra* Leakey et al. [2001] and Cela-Conde and Altaba [2002]). Rather, it simply requires the adaptive zone to be consistent and coherent across the species in the putative genus. That is, in contrast to Mayr (1950), Wood and Collard's (1999) proposal allowed for the possibility that species assigned to different genera will occupy the same adaptive zone, but it prevented species in the same genus from occupying different adaptive zones. Wood and Collard (1999) suggested two criteria for assessing whether or not a group of species has been correctly assigned to a genus. First, the species should belong to the same monophyletic group as the type species of that genus. Second, the adaptive strategy of the species should be closer to the adaptive strategy of the type species of the genus in which it is included than to the type species of any other genus.

The fifth approach to recognizing genera was outlined by Watson et al. (2001). These authors suggested that species should be grouped into genera on the basis of genetic distance. Specifically, Watson et al. (2001) argued that, if the genetic distance between a pair of species is the same as or less than the genetic distance that is typical for congeneric pairs of species in other animal groups, then the species in question should be assigned to the same genus.

The sixth and final approach to the genus concept was outlined by Cela-Conde and Altaba (2002; see also Cela-Conde and Ayala 2003). Their concept is similar to the one advocated by Wood and Collard (1999) in that it holds that a genus should be monophyletic and uses inferences about adaptation to determine which monophyla should be designated genera. However, it differs from Wood and Collard's (1999) concept in that it allows for the species assigned to a genus to occupy more than one adaptive zone. Specifically, Cela-Conde and Altaba (2002) suggested that one species in each genus should be designated as the *species germinalis*. This species is the one that is considered to have given rise to the other species in the genus. Because of its ancestral status, the *species germinalis* is allowed to occupy a different adaptive zone from the other species in the genus.

Several of these concepts have been applied to genus *Homo* in recent years. Hennig's (1966) approach to delineating supraspecific taxa has been applied to

Homo in a series of papers and books produced by a team of researchers led by Morris Goodman (e.g., Goodman et al. 1998, 2001; Wildman et al. 2003). Goodman et al. (1998) averred that, at least among the primates, monophyla should be deemed to be genera if they originated 11–7 Ma before present (Ma BP). Goodman et al. (1998) selected this criterion on the basis of local molecular clock analyses, which suggested that the majority of extant primate genera arose between 11 and 7 Ma BP. Subsequently, Wildman et al. (2003) further justified the selection of 11 to 7 Ma BP as the criterion for recognizing primate monophyla as genera on the grounds that the majority of genera in other mammalian orders arose between 11 and 7 Ma BP. Significantly for present purposes, as Goodman and coworkers have noted on a number of occasions (Goodman et al. 1998, 2001; Wildman et al. 2003), their definition of the genus implies that *Homo* should be broadened to include not only the australopiths and other early hominins, but also chimpanzees and bonobos, which are conventionally assigned to the genus *Pan*. This is because molecular clock studies suggest that humans, chimpanzees and bonobos last shared a common ancestor around 6 Ma BP, and the nomen *Homo* has priority over the nomen *Pan*, the former being proposed by Linnaeus in 1758, as noted earlier, and the latter by Oken in 1816. Subsequently, one of the authors of the Goodman et al. (1998) study, Colin Groves, proposed at least two other time depth-based criteria for recognizing monophyla as genera (Groves 2001a, 2001b; Cameron and Groves 2004). For example, in his widely-cited monographic treatment of primate taxonomy Groves reviewed evidence pertaining to the chronological origin of genera in several mammalian families, including Ursidae, Canidae, Elephantidae, Rhinocerotidae, Hippopotamidae, and Bovidae, and concluded on the basis of this evidence that an origin time of between 7 and 4 Ma BP should be used as the criterion for delineating extant mammalian genera (Groves 2001a). This led him to retain *Homo* and *Pan* as separate genera in contrast to Goodman et al. (1998). More recently, Groves proposed that primate monophyla should be recognized as genera if they originated between 6 and 4 Ma (Cameron and Groves 2004). The corollary of this, he suggested, is that all extinct hominin genera and perhaps also the chimpanzee genus, *Pan*, should be assigned to *Homo*.

In the paper in which Wood and Collard outlined their genus concept (Wood and Collard 1999), they applied the criteria derived from it to the species that most researchers then assigned to genus *Homo*, namely *H erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. They examined a range of phylogenetic and functional evidence in order to determine whether or not the fossil species assigned to *Homo* form a monophylum with *Homo sapiens* and also share its adaptive strategy. They found that the only fossil *Homo* species that form a robust clade with *H. sapiens* are *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus* and *H. ergaster*. They also found that when evidence about body size, body shape, relative brain size and development is combined with inferences about locomotion and diet, these species are the only *Homo* taxa whose adaptations are closer to those of *H. sapiens* than they are to those of *Au. africanus*, the type species of *Australopithecus*. The phylogenetic relationships of *H. habilis* and *H. rudolfensis* were found to be equivocal, and the available evidence regarding the adaptive strategies of *H. habilis* and *H. rudolfensis* was interpreted as indicating that they were at least as similar, and probably more similar, to the australopiths than they are to *H. sapiens*. Wood and Collard (1999) concluded from this that a genus *Homo* that includes them is not a "good" genus, and that *H. habilis* and *H. rudolfensis* should be removed from *Homo* and placed in *Australopithecus* until such time as their phylogenetic relationships are clarified. Recently, Cameron has employed the concept proposed by Wood and Collard (1999), but reached different conclusions regarding the fossil species that should be assigned or excluded to *Homo* (Cameron and Groves 2004). Most notably for present purposes he argued that the *H. habilis* hypodigm should be retained in *Homo*, and suggested that the *H. rudolfensis* hypodigm should be removed from *Homo* and assigned to *Kenyanthropus*. The latter proposal is based on cladistic analyses that link the *H. rudolfensis* hypodigm with *Kenyanthropus platyops* (Cameron and Groves 2004). Cameron does not explain how retaining the *H. habilis* hypodigm within *Homo* is consistent with the notion that a genus should be a species or monophylum whose members occupy a single adaptive zone. However, the implication is that he does not accept Wood and Collard's (1999) contention that the adaptive strategy of *H. habilis* was more similar to that of *Au. africanus* than to the adaptive strategy of *H. sapiens*.

In the 2001 paper in which Watson and colleagues outlined their genetic distance-based concept of the genus they also applied the concept to previously published mtDNA sequence and DNA hybridization data for humans, chimpanzees, gorillas and a range of other mammalian groups with a view to classifying the living hominoids (Watson et al. 2001). They found that the genetic distances between chimpanzees and humans are equivalent to the distances between many mammalian species within the same genus. They also found that the genetic distances between gorillas and chimpanzees, and between gorillas and humans, are similar to the distances between congeneric mammalian species. These observations, Watson et al. (2001) suggested, indicate that the genus *Homo* should be expanded to include chimpanzees and gorillas as well as humans. Watson et al.'s (2001) approach has also been applied to DNA distance data for humans and chimpanzees by Curnoe and Thorne (2003). These authors also concluded that the human and chimpanzee genomes are sufficiently similar for the species to be considered congeneric. Accordingly, they recommended transferring chimpanzees to genus *Homo*.

In 2002, Cela-Conde and Altaba revised the taxonomy for the hominins proposed by Wood and Collard (1999) in the light of their *species germinalis* concept and fossil specimens recovered in the intervening period (Cela-Conde and Altaba 2002). Most significantly for present purposes, Cela-Conde and Altaba (2002) agreed with Wood and Collard (1999) that *H. rudolfensis* should be removed from genus *Homo*, but disagreed with them regarding the generic attribution of *H. habilis*. They suggested that *H. rudolfensis* should be transferred to the genus *Kenyanthropus*, which had been erected in 2001 to accommodate the newly discovered species *K. platyops*, and that *H. habilis* should be included in *Homo* as the *species germinalis* of the genus. In 2003, Cela-Conde and Ayala revised the taxonomy proposed by Cela-Conde and Altaba (2002) (Cela-Conde and

Ayala 2003). They argued not only that *H. habilis* and *H. rudolfensis* should be included in *Homo*, but also that the hypodigm of *K. platyops* should be transferred to *Homo* as the *species germinalis* of the genus. Cela-Conde and Ayala (2003) included the *H. habilis* and *H. rudolfensis* hypodigms in *Homo* on the grounds that they share the morphological traits that Leakey et al. (1964) suggested define *Homo*. The inclusion of the *K. platyops* hypodigm in *Homo* is justified, Cela-Conde and Ayala (2003) argued, because it is similar to *H. habilis* and especially *H. rudolfensis* in certain features of its face and dentition. Cela-Conde and Ayala (2003) designated *platyops* as the *species germinalis* of *Homo* because it lacks "the more advanced features of *Homo* that appear with *Homo erectus* and *Homo ergaster*" (p. 7686).

Table 1 presents a comparison of the definitions put forward by Goodman et al. (1998), Wood and Collard (1999), Watson et al. (2001) and Cela-Conde and Ayala (2003). The first column in the table lists the names of the genera and species recognized in a typical taxonomy covering the hominins and the extant African apes (Stanford et al. 2005). The other columns in the table record the names of the species and genera that would be recognized among the hominins and African apes if the conventional taxonomy were revised in line with the proposals of Goodman et al. (1998), Collard and Wood (1999), Watson et al. (2001) and Cela-Conde and Ayala (2003). The table shows that the four definitions have different implications for not only the composition of genus *Homo* but also the taxonomy of hominins and extant African apes. The conventional taxonomy recognizes 21 species and assigns these to nine genera. Revising the conventional taxonomy in line with Wood and Collard's (1999) and Cela-Conde and Ayala's (2003) proposals results in relatively few changes. Wood and Collard's (1999) scheme leads to species being moved between genera but no reduction in the number of genera, while the one put forward by Cela-Conde and Ayala (2003) requires species to be moved between genera and the elimination of a genus, *Kenyanthropus*. Goodman et al.'s (1998) and Watson et al.'s (2001) proposals have more radical implications. If the conventional taxonomy were to be reorganized in line with Goodman et al.'s (1998) definition of *Homo*, then the 21 species would be assigned to just two genera, *Homo* and *Gorilla*; *Homo* would have 20 species assigned to it, and *Gorilla* a single species. If the conventional taxonomy were reorganized in line with the definition of *Homo* offered by Watson et al. (2001), then the 21 species would be assigned to a single genus. Thus, some proposals to redefine *Homo* have little or no impact on the current consensus regarding generic diversity among the hominins and African apes, while others have a major impact.

The definitions of genus *Homo* presented by Goodman et al. (1998), Wood and Collard (1999), Watson et al. (2001), Cela-Conde and Altaba (2002), and Cela-Conde and Ayala (2003) have other implications for how *Homo* is interpreted. One of the most obvious is the time of its origin. Conventional taxonomies such as the one outlined in Table 1 suggest that the genus arose in the late Pliocene, since the current first appearance dates of *H. habilis* and *H. rudolfensis* are c. 2.35 and c. 2.5 Ma, respectively. Collard and Wood's (1999) definition, which excludes *H. habilis* and *H. rudolfensis* from the genus, implies that *Homo* appeared about 2.0 Ma BP.

Table 1 Illustrative comparison of the impact of four recent proposals to revise genus *Homo* on the taxonomy of hominids and the African apes. A conventional splitter's taxonomy (CST) taken from Stanford et al. (2005) is used as the baseline

CST	CST revised as per Goodman et al. (1998)	CST revised as per Wood and Collard (1999)	CST revised as per Watson et al. (2001)	CST revised as per Cela-Conde and Ayala (2003)
Ardipithecus ramidus	*Homo ramidus*	*Ardipithecus ramidus*	*Homo ramidus*	*Ardipithecus ramidus*
Australopithecus afarensis	*Homo afarensis*	*Australopithecus afarensis*	*Homo afarensis*	*Australopithecus afarensis*
Australopithecus africanus	*Homo africanus*	*Australopithecus africanus*	*Homo africanus*	*Australopithecus africanus*
Australopithecus anamensis	*Homo anamensis*	*Australopithecus anamensis*	*Homo anamensis*	*Australopithecus anamensis*
Australopithecus bahrelghazali	*Homo bahrelghazali*	*Australopithecus bahrelghazali*	*Homo bahrelghazali*	*Australopithecus bahrelghazali*
Australopithecus garhi	*Homo garhi*	*Australopithecus garhi*	*Homo garhi*	*Australopithecus garhi*
Gorilla gorilla	*Gorilla gorilla*	*Gorilla gorilla*	*Homo gorilla*	*Gorilla gorilla*
Homo erectus	*Homo erectus*	*Homo erectus*	*Homo erectus*	*Homo erectus*
Homo habilis	*Homo habilis*	*Australopithecus habilis*	*Homo habilis*	*Homo habilis*
Homo heidelbergensis	*Homo heidelbergensis*	*Homo heidelbergensis*	*Homo heidelbergensis*	*Homo heidelbergensis*
Homo neanderthalensis	*Homo neanderthalensis*	*Homo neanderthalensis*	*Homo neanderthalensis*	*Homo neanderthalensis*

Homo rudolfensis	*Homo rudolfensis*	*Australopithecus rudolfensis*	*Homo rudolfensis*	*Homo rudolfensis*
Homo sapiens	*Homo sapiens*	*Homo sapiens*	*Homo sapiens*	*Homo sapiens*
Kenyanthropus platyops	*Homo platyops*	*Kenyanthropus platyops*	*Homo platyops*	*Homo platyops*
Orrorin tugenensis	*Homo tugenensis*	*Orrorin tugenensis*	*Homo tugenensis*	*Orrorin tugenensis*
Pan paniscus	*Homo paniscus*	*Pan paniscus*	*Homo paniscus*	*Pan paniscus*
Pan troglodytes	*Homo troglodytes*	*Pan troglodytes*	*Homo troglodytes*	*Pan troglodytes*
Paranthropus aethiopicus	*Homo aethiopicus*	*Paranthropus aethiopicus*	*Homo aethiopicus*	*Paranthropus aethiopicus*
Paranthropus boisei	*Homo boisei*	*Paranthropus boisei*	*Homo boisei*	*Paranthropus boisei*
Paranthropus robustus	*Homo robustus*	*Paranthropus robustus*	*Homo robustus*	*Paranthropus robustus*
Sahelanthropus tchadensis	*Homo tchadensis*	*Sahelanthropus tchadensis*	*Homo tchadensis*	*Sahelanthropus tchadensis*

In contrast, the other three definitions push back the date of origin. Cela-Conde and Ayala's (2003) definition implies that the genus appeared around 3.5 Ma, which is the date of the *species germinalis* they propose for *Homo*, *H. platyops* (Leakey et al. 2001). The definitions put forward by Goodman et al. (1998) and Watson et al. (2001) imply that the genus originated even earlier. The timing of the spit between the lineage leading to chimpanzees and the lineage leading to modern humans split is still under investigation, as is the timing of the split between the lineage leading to gorillas and the lineage leading to chimpanzees and modern humans. But it is generally accepted that both events occurred long before 3.5 Ma. Estimates in the range of 5.5–8 Ma for the chimp-human split and 8.5–12 Ma for the gorilla-chimp/human split are typical (e.g., Scally et al. 2012). Thus, if we accept Goodman et al.'s (1998) definition genus *Homo* originated by at least 5.5 Ma, while if we accept Watson et al.'s (2001) definition it originated by at least 8.5 Ma.

Another aspect of the genus that varies considerably depending on the definition employed is its mode of locomotion. Conventional taxonomies incorporate at least two forms of locomotion, facultative bipedalism and obligate bipedalism. The extinct hominin species Wood and Collard (1999) assign to *Homo* are all reconstructed as being obligate bipeds, while Goodman et al.'s (1998) and Watson et al.'s (2001) definitions incorporate obligate bipeds, facultative bipeds and knuckle-walkers within genus *Homo*. Most of the other adaptive characteristics that are of interest to paleoanthropologists, such as the size of the masticatory system, brain size and developmental schedule are affected in a similar manner.

Given that these various genus concepts evidently have markedly different implications for the composition, and therefore the interpretation, of *Homo*, which of them should be preferred? In our view, the approach to delineating genera proposed by Watson et al. (2001) is not convincing. The notion that genetic distances among congeneric species in one animal group should be used as a criterion to cluster species into genera in another animal group is problematic. First, given that there does not seem to be a straightforward relationship between genetic distance and morphological distance among living taxa (Lambert and Paterson 1993), it is doubtful that Watson et al.'s (2001) suggestions can be applied to fossil taxa. Second, even if it were possible to obtain reliable estimates of the genetic distances among pairs of fossil species, there is no reason to believe that interspecific genetic distances are distributed in such a way as to justify designating any particular distance or range of distances as the criterion for clustering species into genera. This course of action might be appropriate if interspecific genetic distances were discontinuously distributed or if there were sound theoretical reasons why genera should correspond to a given genetic distance. However, neither of these conditions appears to be the case. The available evidence suggests that genetic distances are more or less continuously distributed (Lambert and Paterson 1993), and Watson et al. (2001) do not provide any theoretical justification for the approach they advocate. Accordingly, there is no reason to prefer one particular genetic distance or range of distances as the criterion for delineating genera over any other genetic distance or range of distances.

We are also skeptical about the utility of the hybridizability-based concept for assigning species to genus *Homo*. Given that many of the relevant species are known only from fossilized bones, application of this concept requires skeletal variation among hominins to be a reliable proxy for hybridizability. This assumption is only valid if skeletal variation has been found to accurately predict hybridizability in a range of appropriate model taxa such as the living primates. The relationship between skeletal variation and hybridizability has been investigated in a few animal groups (Ackermann 2010; Ackermann and Bishop 2010), but there is good reason to doubt that the relationship between these parameters in primates is such that the hybridizability-based concept can be used to assign species to genus *Homo*. In the last 20 years a number of studies have demonstrated that there is considerable overlap between intraspecific and interspecific skeletal variation in living primates (Tattersall 1986; Kimbel 1991; Aiello et al. 2000). Given that species status has been conferred on most extant primate species on the basis of failure to produce fertile offspring in the wild, this overlap suggests that skeletal morphology is a poor guide to reproductive biology in primates. Accordingly, it seems unlikely that skeletal morphology can be used to assign fossil hominin species to *Homo* on the basis of their likely ability to produce viable hybrids.

Hennig's (1966) approach to delineating genera and other supraspecific taxa has the advantage that it is relatively easy to implement. Another advantage of Hennig's approach for paleoanthropology, at least in the way it has been implemented by Goodman et al. (1998), is that the genera it produces can be expected to be relatively stable. Given that, as discussed earlier, the consensus is that the split between the human and chimpanzee lineages occurred no earlier than 8 Ma, Goodman et al.'s (1998) proposal that monophyla should be recognized as genera if they originated between 11 and 7 Ma means that new fossil hominin finds and fresh phylogenetic analyses will rarely require the creation of new genera.

However, the time-based approach also has a number of shortcomings. One of these concerns the manner in which the time ranges that correspond to different taxonomic ranks are chosen. As noted earlier, the approach that is most defensible on theoretical grounds – strict application of the time of origin criterion across all groups – was considered to be impractical even by Hennig. Unfortunately, the alternative approach proposed by Goodman et al. (1998) and Groves (2001a) – assigning taxa in one group of organisms (e.g., primates) to ranks on the basis of the age of origin of taxa within another group of organisms (e.g., bears) – is problematic. One problem is that the approach is sensitive to the choice of comparator groups. For example, Goodman et al. (1998) review one set of first appearance dates and conclude that monophyla should be recognized as genera if they originate between 11 and 7 Ma, while Groves (2001a) reviews another set of first appearance dates and concludes that the relevant time span should be 6–4 Ma. It is difficult to see how this can be avoided given that phylogenetic relationships are relative phenomena. How do we defend a given degree of relatedness as the criterion for deciding which taxa to include in our comparator group and which to exclude?

A second and perhaps even more profound problem with the approach proposed by Goodman et al. (1998) and Groves (2001a) is that it is not internally consistent.

Again, the problem lies with the comparator taxa. Given that, as we noted earlier, strict application of the time of origin across all groups is impractical, at least one of the comparator taxa must be defined in relation to a criterion other than time, such as adaptive coherence. For example, as noted earlier, Groves (2001a) assigns primate species to genera in the light of the first appearance dates of genera in Ursidae, Canidae, Elephantidae, Rhinocerotidae, and Hippopotamidae, but it is evident from the references he cites in relation to the latter that they have been defined on the basis of anatomical evidence. Thus, the approach advocated by Goodman et al. (1998) and Groves (2001a) essentially entails reorganizing the taxonomy of one group of organisms on the basis of prior taxonomic analyses of another group of organisms that employed a different approach to delineating taxa. We recognize that, in the absence of a strict application of the time of origin across all groups, this is unavoidable, but it is still a major flaw. It means that the approach is not only contradictory (time of origin is the preferred criterion for assigning taxa to ranks *except* in the case of the comparator taxa, which are defined in relation to some other criterion), but it also effectively requires paleoanthropologists to subjugate their own taxonomic philosophies in favor of those used by researchers working on other groups of organisms.

The differences between the remaining approaches are subtle. To reiterate, for Mayr (1950) a genus is a species or group of species of common descent that occupies an ecological situation that is different from those occupied by the species of another genus, while for Wood and Collard (1999) a genus is a species or monophylum whose members occupy a single adaptive zone. Cela-Conde and Altaba's (2002) concept is similar to the one proposed by Wood and Collard (1999) in that it holds that the species assigned to a genus should be monophyletic and uses inferences about adaptation to determine which monophyla should be designated genera. However, it differs from Wood and Collard's (1999) concept in that one species, the *species germinalis*, is allowed to occupy a different adaptive zone from the other species in the genus. Thus, the approaches differ regarding whether phylogeny should be given priority over adaptation or vice versa. Mayr's (1950) approach prioritizes species' adaptive characteristics over their phylogenetic relationships; Wood and Collard's (1999) approach prioritizes species' phylogenetic relationships, but also takes into account their adaptive characteristics; Cela-Conde and Altaba's (2002) approach prioritizes species' phylogenetic relationships over their adaptive characteristics. One important consequence of these differences is that Mayr's (1950) approach allows genera to be either monophyletic or paraphyletic, whereas the approaches favored by Wood and Collard (1999) and Cela-Conde and Altaba (2002) hold that genera must be monophyletic. Another important consequence is that Wood and Collard's (1999) approach makes allowance for the possibility that species in different genera will occupy the same adaptive zone, whereas Mayr's (1950) approach demands that species assigned to different genera must have different adaptive strategies. In contrast to both Mayr's (1950) approach and the one put forward by Wood and Collard (1999), Cela-Conde and Altaba's (2002) approach anticipates that the species assigned to a genus may subsume two adaptive strategies – the ancestral adaptive strategy, which will be displayed by the *species germinalis*, and the derived adaptive strategy, which will be exhibited by the remaining species.

Choosing between the genus concepts proposed by Mayr (1950), Wood and Collard (1999) and Cela-Conde and Altaba (2002) is not straightforward. It is especially difficult for paleoanthropologists, given that we often need to classify taxa based on a few specimens, and occasionally just a single specimen. The dilemma with which we are confronted was outlined particularly clearly by Alan Walker in a paper titled "Remains attributable to *Australopithecus* in the East Rudolf succession," published in 1976. Walker pointed out that while classifying fossil hominins on the basis of their adaptive characteristics is problematic, so too is classifying them on the basis of their phylogenetic relationships. The former is problematic because, if the approach is followed to its logical conclusion, there will come a point where one generation is in one taxon and the next in another. The latter is problematic because, if its logic is followed, there will come a point where part of a single population will be in one taxon and another part of the same population will be in a different taxon. None of three remaining genus concepts avoids this dilemma. Ultimately, they all force researchers to choose to err in one direction or the other. Indeed, given that evolution involves both descent and modification, it is difficult to see how it could be otherwise. Thus, it is not easy to choose between the three concepts on theoretical grounds.

Choosing between the concepts on practical grounds is also difficult. Given that one of the main purposes of a biological classification is to communicate information about taxa (Harrison 1993), the key practical issues would seem to be stability, minimizing the number of genera, and the transparency and utility of the criteria used for delineating genera. Mayr's (1950) approach can be expected to be more stable than the approaches put forward by Wood and Collard (1999) and Cela-Conde and Altaba (2002). This is because Mayr's (1950) approach allows genera to be either monophyletic or paraphyletic, whereas the approaches of Wood and Collard (1999) and Cela-Conde and Altaba (2002) require genera to be monophyletic. The ability of Mayr's (1950) approach to take into account paraphyletic taxa means that the genera it produces are less likely to need revising in the light of new fossil finds or fresh phylogenetic analyses than the genera produced by Wood and Collard's (1999) and Cela-Conde and Altaba's (2002) approaches. The ability of Mayr's (1950) approach to take into account paraphyletic taxa also means that it can be expected to result in fewer genera than the approaches of Wood and Collard (1999) and Cela-Conde and Altaba (2002). Cela-Conde and Altaba's (2002) approach can also be expected to result in fewer genera than the approach put forward by Wood and Collard (1999), because the species that Cela-Conde and Altaba (2002) designate as the *species germinalis* would be assigned to a new genus in Wood and Collard's (1999) approach. Thus, in terms of stability and minimizing genera, Mayr's (1950) approach is to be preferred over the approaches put forward by Cela-Conde and Altaba (2002), which in turn is to be preferred over Wood and Collard's (1999) approach.

However, Wood and Collard's (1999) approach has the advantage with respect to the explicitness of the criteria for delineating genera. As noted earlier, Wood and

Collard (1999) suggest that the fossil species assigned to genus *Homo* should be (1) more closely related to the type species of the genus, *H. sapiens*, than to the type species of any other genus, and (2) more similar to *H. sapiens* than to the type species of any other genus in terms of key adaptive variables. The ones they proposed – body mass, body shape, locomotion, size of the teeth and jaws, relative brain size, and developmental schedule – are all capable of being inferred with a reasonable degree of reliability from the fossil record. In contrast, neither Mayr (1950) nor Cela-Conde and Altaba (2002) provided workable criteria for delineating genera. Mayr (1950) suggested that the species assigned to a genus should be separated from other groups of species by a "decided morphological gap" and also occupy a "different ecological situation," but he did not specify what constitutes a decided morphological gap or a different ecological situation. Cela-Conde and Altaba (2002) proposed that a genus should be a monophylum whose members are adaptively distinct apart from the *species germinalis*, which is allowed to have the same adaptive strategy as another genus. But they did not provide criteria for determining that a group of species is adaptively distinct from another group of species. They also did not provide criteria for identifying the *species germinalis*. Needless to say, the lack of adequate criteria for delineating genera makes it difficult to implement the approaches put forward by Mayr (1950) and Cela-Conde and Altaba (2002). It also makes the resulting taxonomies difficult to defend. For example, Cela-Conde and Ayala (2003) revise Cela-Conde and Altaba's (2002) taxonomy without recourse to analysis. Accordingly, for the time being (i.e., until Mayr's [1950] and Cela-Conde and Altaba's [2002] approaches are operationalized satisfactorily) our preference is to use the approach outlined by Wood and Collard (1999).

Updating Wood and Collard's (1999) Review of Genus *Homo*

With the last point of the foregoing section in mind, the remainder of this chapter is devoted to updating Wood and Collard's (1999) review of genus *Homo* in the light of developments since their study appeared. To reiterate, Wood and Collard (1999) applied their genus concept to the species that most researchers assigned to genus *Homo* in the late 1990s, namely *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. They examined a range of phylogenetic and functional evidence in order to determine whether or not the fossil species assigned to *Homo* form a monophylum with *Homo sapiens* and also share its adaptive strategy. They suggested that the only fossil *Homo* species that form a robust clade with *H. sapiens* are *H. neanderthalensis*, *H. heidelbergensis*, *H. erectus* and *H. ergaster*. They also found that when evidence about body size, body shape, relative brain size and development is combined with inferences about locomotion and diet, these are the only *Homo* species whose adaptations are closer to those of *H. sapiens* than they are to *Au. africanus*, the type species of *Australopithecus*, or *P. robustus*, the type species of *Paranthropus*. Wood and Collard (1999) found the phylogenetic relationships of *H. habilis* and

H. rudolfensis to be equivocal, and interpreted the available evidence regarding the adaptive strategies of *H. habilis* and *H. rudolfensis* as indicating that they are more similar to *Au. africanus* than they are to *H. sapiens*. Wood and Collard (1999) concluded from this that *Homo* as thus constituted is not a "good" genus, and that *H. habilis* and *H. rudolfensis* should be removed from genus *Homo* and placed in *Australopithecus* until such time as their phylogenetic relationships are clarified.

Wood and Collard's (1999) conclusions regarding their phylogenetic criterion were based on the results of the six studies that had, at the time of writing, included enough fossil hominin species to adequately test the monophyly of *Homo* (Chamberlain 1987; Chamberlain and Wood 1987; Wood 1991, 1992; Lieberman et al. 1996; Strait et al. 1997) as well as re-analyses of the datasets used in three of the studies (Wood 1991, 1992; Strait et al. 1997). Since Wood and Collard's (1999) study appeared, a further six phylogenetic studies have included sufficient fossil hominin species to assess the hypothesis that the species assigned to genus *Homo* form a monophyletic unit (Curnoe 2001; Cameron and Groves 2004; Strait and Grine 2004; Gonzalez-Jose et al. 2008; Argue et al. 2009; Irish et al. 2013).

Curnoe (2001) focused on the phylogenetic relationships of three specimens from South Africa, SK 847, SK15 and Stw 53, all of which are usually considered to represent early *Homo*. His analysis employed 47 cranial characters recorded on SK 847, SK15, Stw 53 plus specimens assigned to *Australopithecus afarensis*, *Au. africanus*, *H. erectus*, *H. habilis*, *H. rudolfensis*, *Paranthropus aethiopicus*, *P. robustus*, and *P. boisei*. He used the same data set in six analyses, in which methodological choices were varied in order to avoid bias. The common chimpanzee, *Pan troglodytes*, was used as the outgroup in all the analyses. The results of Curnoe's analyses do not support the hypothesis that *Homo* is a monophylum. Both the most parsimonious cladogram and the consensus cladogram presented by Curnoe (2001) suggest that *H. habilis*, *H. erectus* and the three South African early *Homo* specimens form a clade to the exclusion of the other taxa in the sample. However, *H. rudolfensis* is not linked exclusively to the other *Homo* taxa in any of the cladograms presented by Curnoe (2001). In two of them (A and D in Curnoe's [2001], Fig. 1), it is the sister taxon of a clade comprising *Au. africanus* and the other *Homo* taxa. In another two (B and C in Curnoe's [2001], Fig. 1) it is part of a large polychotomy that also contains *Au. africanus*. In the remaining cladogram (E in Curnoe's [2001], Fig. 1), *H. rudolfensis* forms a clade with *P. boisei* and *P. robustus*.

Cameron and Groves (2004) examined the phylogenetic relationships of 14 hominin species, including *H. ergaster*, *H. habilis*, *H. rudolfensis* and *H. sapiens*. They carried out two sets of analyses. One employed 92 characters; the other utilized only the characters that were present in *Sahelanthropus tchadensis* or *K. platyops*, of which there were 52. In both sets of analyses, three Miocene ape species were employed as outgroups. A parsimony analysis of the 92 characters returned eight equally parsimonious trees. The consensus of these clustered *H. ergaster*, *H. habilis* and *H. sapiens* in a clade to the exclusion of the other taxa, and grouped *H. rudolfensis* in a clade with *K. platyops*. A bootstrap analysis of the 92 characters supported a sister group relationship between

H. ergaster and *H. sapiens*, but was unable to resolve the relationships of the other *Homo* taxa at the 70% level of support that is commonly used to identify statistically significant clades in such analyses (Hillis and Bull 1993). *Homo habilis* and *H. rudolfensis* formed a multichotomy with *K. platyops*, *Au. africanus*, a clade comprising *P. aethiopicus*, *P. boisei* and *P. robustus*, and the aforementioned (*H. ergaster*, *H. sapiens*) clade. The results of the 52 character analyses were similar. Twenty equally parsimonious cladograms were returned by a parsimony analysis. The consensus of these grouped *H. ergaster*, *H. habilis* and *H. sapiens* in a clade to the exclusion of the other taxa, and clustered *H. rudolfensis* in a clade with *K. platyops*. A bootstrap analysis supported a sister group relationship between *H. ergaster* and *H. sapiens*, but was unable to resolve the relationships of the other *Homo* taxa at the 70% level. Thus, neither set of analyses supported the hypothesis that the fossil species assigned to *Homo* form a monophyletic group with *H. sapiens*. They suggest that *H. ergaster* is more closely related to *H. sapiens* than to any other fossil hominin species, but are equivocal regarding the relationships of *H. habilis* and *H. rudolfensis*.

Strait and Grine (2004) carried out a series of maximum parsimony and bootstrap analyses to examine the relationships of several hominin species including *H. ergaster*, *H. habilis*, *H. rudolfensis* and *H. sapiens*. Their dataset comprised 109 qualitative craniodental characters and 89 craniometric characters recorded on 14 hominin species plus seven extant non-human primate taxa. The consensus of the most parsimonious cladograms obtained by Strait and Grine (2004) suggests that *H. ergaster*, *H. habilis*, *H. rudolfensis* and *H. sapiens* form a clade to the exclusion of the other species in the sample. Within the (*H. ergaster*, *H. habilis*, *H. rudolfensis*, *H. sapiens*) clade, *H. ergaster* and *H. sapiens* form a clade to the exclusion of *H. habilis* and *H. rudolfensis*. The relationships among the (*H. ergaster*, *H. sapiens*) clade, *H. habilis* and *H. rudolfensis* are unresolved. The results of Strait and Grine's (2004) bootstrap analyses were inconsistent with regard to the relationships of the *Homo* species. When all the characters and taxa were analyzed together, a (*H. ergaster*, *H. sapiens*) clade was supported by 86% of the bootstrap replicates, but the relationships of the other *Homo* taxa were not resolved at the 70% level. A similar result was obtained when all the taxa but only the 109 qualitative characters were included. When *K. platyops* was dropped from the all-characters analysis, both a (*H. ergaster*, *H. sapiens*) clade and a (*H. ergaster*, *H. habilis*, *H. rudolfensis*, *H. sapiens*) clade were supported by more than 70% of the replicates. Again, a similar result was obtained when only the qualitative characters were included. Thus, Strait and Grine's (2004) parsimony analyses support the hypothesis that *Homo* is a monophylum, but this hypothesis is not consistently supported by their bootstrap analyses. Smith and Grine (2008) reanalyzed Strait and Grine's (2004) dataset to assess the relationships of some controversial early *Homo* specimens from southern Africa, and obtained similar results.

The study reported by Gonzalez-Jose et al. (2008) sought to recover a phylogenetic signal from three-dimensional geometric morphometric data recorded on 18 hominin crania and two great ape crania. The shape data were subjected to principal components analysis, and then the principal component scores were included as variables in a maximum parsimony analysis and a maximum likelihood analysis. Only the first of these analyses included sufficient hominin species to assess the monophyletic status of genus *Homo*. This analysis returned a single most parsimonious cladogram in which the various *Homo* specimens were shown as more closely related to each other than any of them is to specimens assigned to other genera.

Argue et al.'s (2009) study focused on the phylogenetic position of the controversial fossil hominin taxon, *Homo floresiensis*. Their dataset consisted of states for 60 cranial characters scored on specimens assigned to ten hominin taxa and three outgroup species. In addition to *H. floresiensis*, the hominin taxa included *Au. afarensis*, *Au. africanus*, *H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, *Homo rhodesiensis* (a junior synonym of *Homo heidelbergensis*), a sample of early *Homo* fossils from Dmanisi, and *H sapiens*. Argue et al. (2009) subjected their dataset to maximum parsimony analysis and bootstrapping. The maximum parsimony analyses returned two most parsimonious cladograms. Both of these suggested that the *Homo* taxa in their sample are more closely related to each other than any of them is to the other species in their sample, *Au. afarensis* and *Au. africanus*. However, none of the bootstrap support values for the clades of the most parsimonious cladograms exceeded or even equaled 70%. This indicates that the dataset contains a large number of homoplastic similarities and does not support any of the relationships suggested by the most parsimonious cladograms. Thus, Argue et al.'s (2009) study does not support the hypothesis that the species assigned to *Homo* form a monophyletic unit.

The goal of Irish et al.'s (2013) study was to elucidate the phylogenetic relationships of the relatively new fossil hominin species *Australopithecus sediba*. Their dataset comprised 23 dental traits recorded on ten hominin species plus an outgroup, *Gorilla gorilla*, and they subjected the dataset to both maximum parsimony analysis and 10,000-replication bootstrap analysis. Irish et al.'s (2013) most parsimonious cladogram supports the monophyly of genus *Homo*, because the four *Homo* taxa in their sample (*H. habilis/rudolfensis*, *H. erectus*, sub-Saharan *H. sapiens*, north African *H sapiens*) are grouped together to the exclusion of all the other fossil hominin species in their sample. However, none of the bootstrap support values for the clades of the most parsimonious cladogram exceeds 50% let alone 70%. So, the Irish et al. (2013) study also cannot be counted as supporting the hypothesis that the species assigned to *Homo* form a monophyletic unit.

Collectively, the studies of Curnoe (2001), Cameron and Groves (2004), Strait and Grine (2004), Gonzalez-Jose et al. (2008), Argue et al. (2009), and Irish et al. (2013) present a similar picture regarding the monophyletic status of *Homo* to the studies reviewed by Wood and Collard (1999). They provide reasonably strong to strong support for considering *H. ergaster*, *H. erectus*, *H. heidelbergensis*, and *H. neanderthalensis* to be more closely related to *H. sapiens* than to the types species of any other genus, but only weak support for the hypothesis that *H. habilis* and *H. rudolfensis* are more closely related to *H. sapiens* than to the types species of any other genus. *Homo rudolfensis* clustered exclusively with the other *Homo* species in Strait and Grine's (2004) parsimony analyses and also in some of their bootstrap analyses, but it did not cluster exclusively with the other *Homo* species in the parsimony and bootstrap analyses reported by Curnoe (2001) and Cameron and Groves (2004). The results of the parsimony analyses carried out by Curnoe (2001), Cameron and Groves (2004), and Strait and Grine (2004) offer support for the hypothesis that *H. habilis* is a member of the *Homo* clade. However, the bootstrap analyses carried out by Cameron and Groves (2004) and some of the bootstrap analyses conducted by Strait and Grine (2004), failed to support a link between *H. habilis* and later *Homo* species at the 70% level. This suggests that little confidence can be placed in this hypothesis. Argue et al.'s (2009) and Irish et al.'s (2013) results also do not support the idea that *H. habilis* and *H. rudolfensis* are more closely related to the other species assigned to *Homo* than to species assigned to other genera. Their maximum parsimony analyses linked *H. habilis* and *H. rudolfensis* taxon with *H. sapiens*, but their bootstrap analyses indicated that this grouping is not supported by their datasets. Thus, on balance, the results of the six new studies have not increased confidence in the hypothesis that the species assigned to *Homo* form a monophyletic unit.

Other developments have challenged Wood and Collard's (1999) conclusions regarding the status of *H. habilis* and *H. rudolfensis* as members of genus *Homo*. Probably the most significant of these was presented in Lordkipanidze et al. (2013). In this paper, David Lordkipandze and his collaborators describe an adult hominin cranium, D4500, recovered from layer B1y in Block 2 at the site of Dmanisi, Georgia. They also report a geometric morphometrics-based analysis that they claim demonstrates that the variation in the sample of fossil hominin crania from Dmanisi exceeds that of *H. habilis*, *H. rudolfensis*, *H. ergaster*, and *H. erectus* combined. The corollary of this, they contend, is that *H. habilis*, *H. rudolfensis*, *H. ergaster*, *H. erectus*, and the Dmanisi specimens should be treated as a single early *Homo* species, the name of which should be *H. erectus*, according to the rules of zoological nomenclature. Obviously, if the hypodigms of *H. habilis* and *H. rudolfensis* are lumped together with those of *H. ergaster* and *H. erectus*, the issue of whether *H. habilis* and *H. rudolfensis* should be assigned to *Homo* or some other genus is rendered null and void. However, Lordkipanidze et al.'s (2013) claim is not defensible. Even if one accepts that their methods of data capture are sound – which we do not – their conclusions are based on a flawed analysis and a logical fallacy. The analytical flaw is that their method fails to distinguish between a morphologically very distinctive and large-brained Neanderthal cranium and the small-brained Dmanisi Skull 4. These specimens are separated by close to two million years of evolutionary history, and are widely accepted to belong to distinct species. That the landmarks Lordkipanidze et al. (2013) employ are unable to distinguish them strongly suggests that the landmarks are inadequate for assessing the limits of fossil hominin species. The logical fallacy is that they take three-dimensional cranial shape to be the arbiter of early hominin taxonomy, yet many of the features that have been used to distinguish *H. habilis*, *H. rudolfensis*, *H. ergaster*, and *H. erectus* (e.g., detailed basicranial morphology, bony labyrinth morphology, foot morphology, long bone strength, life history, relative tooth size) are not captured in such an analysis. There is no justification for claiming to refute a taxonomic hypothesis when the grounds for doing so are so limited.

Wood and Collard's (1999) conclusions regarding the status of *H. habilis* and *H. rudolfensis* as members of genus *Homo* have also been challenged by Antón and Snodgrass (2012). These authors contend that recent work has shown that relative hind-limb length is more similar in *Australopithecus* and *Homo* than appeared to be the case when Wood and Collard (1999) carried out their review. The corollary of this, Antón and Snodgrass (2012) suggest, is that the difference Wood and Collard (1999) identified between *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* on the one hand, and *Australopithecus* and *Homo habilis* on the other hand, is no longer tenable. Again, this obviously represents a potentially serious problem for the hypothesis that *H. habilis* and *H. rudolfensis* should be assigned to a different genus or pair of genera from the other species currently assigned to *Homo*. However, the problem is more apparent than real.

Antón and Snodgrass (2012) base their argument on analyses reported by Pontzer (2012). It is certainly the case that Pontzer (2012) concludes that there is no difference between *Australopithecus* and *Homo* in relation to relative hind-limb length. But this conclusion is based on questionable data. The finding that *Australopithecus* and *Homo* do not differ in relative hind-limb length is primarily based on estimates for putatively large-bodied specimens assigned to *Australopithecus afarensis* (KSD-VP-1/1), *Au. sediba*, and *Au. garhi*. All of the estimates in question are problematic. The *Au. afarensis* specimen KSD-VP-1/1 does not have a femur. It only has a tibia, which means the hind-limb length estimate is not secure. In addition, as the describers of KSD-VP-1/1 make clear (Haile-Selassie et al. 2010), the state of preservation of the specimen's remaining acetabulum is such that its diameter is consistent with a wide range of body mass estimates, some of which can be expected to be much smaller than the estimate utilized by Pontzer (2012). Relative hind-limb length in *Au. sediba* is no more secure. Pontzer (2012) cites body mass estimates of 31.5 kg for MH1 and 35.7 kg for MH2. He indicates that Trenton W. Holliday provided the MH 1 estimate, while the MH 2 estimate was taken from Berger et al. (2010). Neither of these estimates can be relied on. While Holliday is apparently willing to offer a body mass estimate for MH 1, the specimen's femoral head is sufficiently badly damaged that other members of the team involved in the analysis of the Malapa specimens think it is too soon to offer a body mass estimate for the specimen (S. Churchill, personal communication). The body mass estimate for MH 2 that Pontzer (2012) suggests he obtained from Berger et al. (2010) is not in fact included among the data reported by Berger et al. (2010). All Berger et al. (2010) say about body size in *Au. sediba* is that it is "small" (their Table S2). Lastly, the body mass estimate for *Au. garhi* has to be treated with considerable caution because the relevant specimen, BOU-VP-12/1, does not include diagnostic cranial remains and therefore cannot be confidently allocated to a species (Asfaw et al. 1999). Given these problems, plus his uncritical inclusion of KNM-ER 1471 and 1482 in H. habilis, we suggest Pontzer's (2012) claim that there is no difference in relative hind-limb length between *Australopithecus* and

Homo does not hold water. The corollary of this is that there is no basis for Antón and Snodgrass (2012) to challenge Wood and Collard's (1999) conclusions.

The proposed inclusion of the collection of Late Pleistocene specimens from the site of Liang Bua, Flores, in genus *Homo* as a new species, *H. floresiensis* (Brown et al. 2004) represents a third important challenge to Wood and Collard's (1999) conclusions. In justifying the inclusion of the Liang Bua material in *Homo*, Brown et al. (2004) cited Wood and Collard's (1999) study in such a way that it appears that incorporating the *H. floresiensis* hypodigm in *Homo* is compatible with the latter authors' proposals regarding the definition and composition of the genus. However, it is not clear that this is in fact the case.

To begin with, it is not possible to determine whether or not *H. floresiensis* fulfills Wood and Collard's (1999) first criterion for including a species within the genus *Homo*, namely that it is more closely related to *H. sapiens* than to the type species of any other genus. So far, *H. floresiensis* has been the focus of a single phylogenetic study (Argue et al. 2009). The results of this study were, as discussed earlier, ambiguous. To reiterate, the two most parsimonious cladograms obtained by the authors grouped *H. floresiensis* with the other *Homo* species, but none of the bootstrap support values for the clades of the most parsimonious cladograms exceeded or even equaled 70%. This indicates that the dataset contains a large number of homoplastic similarities and does not support any of the relationships suggested by the most parsimonious cladogram. Thus, the phylogenetic relationships of *H. floresiensis* are unclear at the moment.

Some evidence relevant to Wood and Collard's (1999) second criterion – that the adaptive strategies of fossil species assigned to *Homo* should be more similar to that of *H. sapiens* than to the adaptive strategies of the type species of other genera – is available for *H. floresiensis*, but this evidence is difficult to interpret. The individual represented by the partial associated skeleton LB1 has been estimated to have been around 106 cm in height and to have weighed between 16 and 36 kg, depending on the body mass proxy employed (Brown et al. 2004). A tibia belonging to another individual (LB8) is consistent with a stature of 109 cm (Morwood et al. 2005). These figures suggest that *H. floresiensis* was more similar in size to the australopiths than to *H. sapiens*. It also appears that *H. floresiensis* had a relatively small brain. When Wood and Collard's (1999) approach to computing relative brain size (cube root of brain size divided by square root of orbital area, product multiplied by 10) is employed, *H. floresiensis* has a relative brain size that is smaller than those of *Au. africanus*, *P. aethiopicus*, and *P. boisei* (Table 2). Initially, the postcranial anatomy of *H. floresiensis* was suggested to be consistent with the type of obligate bipedalism seen in modern humans as opposed to the form of facultative bipedalism that most researchers believe the australopiths employed (Brown et al. 2004). However, new specimens from Liang Bua, including additional elements of the LB1 associated skeleton, have cast doubt on this hypothesis (Morwood et al. 2005). It now appears that the humerofemoral index of *H. floresiensis* is more similar to that of *Au. afarensis* than it is to that of *H. sapiens* (Morwood et al. 2005). Likewise, Morwood et al. (2005) have suggested that the ilium of LB1 is consistent with a teardrop-shaped thorax rather than the

Table 2 Relative brain size

Taxon	Absolute/cm^3	Orbital area/cm^2	Relative
P. aethiopicus	410	968	2.39
P. boisei	513	1114	2.40
Au. africanus	457	839	2.66
H. habilis	552	908	2.72
H. ergaster	854	1180	2.76
H. rudolfensis	752	1084	2.76
H. heidelbergensis	1198	1403	2.84
H. erectus	1016	1225	2.87
H. neanderthalensis	1512	1404	3.06
H. sapiens	1355	1289	3.08
H. floresiensis	417	992	2.37

Values taken from Wood and Collard (1999) apart from those for *H. floresiensis*. The brain size figure for *H. floresiensis* was taken from Falk et al. (2005). The orbital area figure for this species was obtained by multiplying the values for orbital height and width provided by Brown et al. (2004). Relative brain size was computed by dividing the cube root of absolute brain size by the square root of orbital area and multiplying the product by 10, as per Wood and Collard (1999)

barrel-shaped thoracic region found in modern humans. Morwood et al. (2005) also report that LB1's femoral robusticity falls in the chimpanzee range, and that its humeral robusticity is midway between the chimpanzee range and the human range. These observations suggest that the locomotor behavior of *H. floresiensis* may have been more like that of the australopiths than that of modern humans. However, LB1 apparently differs from all other known hominin species in humeral torsion and aspects of ulna morphology (Morwood et al. 2005), which suggests that this hypothesis may also need to be revised in future. Thus, in terms of body size, relative brain size and inferred locomotor behavior *H. floresiensis* appears to be more similar to the australopiths than to the species that Wood and Collard (1999) assign to genus *Homo*.

The available data pertaining to masticatory morphology presents a different picture. Wood and Collard (1999) assessed masticatory system similarities among the hominins on the basis of Euclidean distances derived from 11 size-corrected dental and mandibular variables. So far, data for only six of these variables have been published for *H. floresiensis* (Brown et al. 2004). When Wood and Collard's analysis is replicated with the six variables, the Euclidean distance between *H. floresiensis* and *H. sapiens* is 1.77, while the comparable distances between *H. floresiensis* and *Au. africanus* and between *H. floresiensis* and *P. robustus* are 4.97 and 5.72, respectively (Tables 3 and 4). Thus, this aspect of the masticatory apparatus of *H. floresiensis* is more similar in size to that of *H. sapiens* than it is to the type species of the other two hominin genera for which Wood and Collard (1999) provide data.

While the lack of clarity about the phylogenetic relationships of *H. floresiensis* precludes a satisfactory assessment of its attribution to *Homo* as per Wood and

Table 3 Masticatory system relative size

Taxon	1	2	3	4	5	6	OA
Au. africanus	41	20	33	23	12.9	14.1	838.95
P. boisei	51	29	42	29	15.7	18.5	1114.26
P. robustus	50	28	39	27	14.1	15.7	1066.42
H. erectus	37	19	36	22	12.0	12.7	1225.33
H. ergaster	33	20	31	19	11.6	12.3	1180.20
H. habilis	27	19	29	21	12.3	12.6	907.68
H. neanderthalensis	42	15	34	18	10.7	10.7	1403.98
H. rudolfensis	36	23	36	23	13.2	13.7	1084.16
H. sapiens	34	14	29	13	10.5	10.5	1289.37
H. floresiensis	28	15	20.5	15.5	11.4	10.0	992.00

Values taken from Wood and Collard (1999) apart from those for *H. floresiensis*. Figures for the mandibular and dental characters for *H. floresiensis* were obtained from Brown et al. (2004). The orbital area value for this species was obtained by multiplying the values for orbital height and width provided by Brown et al. (2004)

1 symphyseal height, *2* symphyseal breadth, *3* corpus height at M_1, *4* corpus width at M_1, *5* M_1 buccolingual diameter, *6* M_2 buccolingual diameter, *OA* orbital area

Table 4 Normalized Euclidean distances between fossil *Homo* species and *H. sapiens*, *Au. africanus* and *P. robustus* based on the masticatory system variable values given in this table

	H. sapiens	*Au. africanus*	*P. robustus*
H. rudolfensis	3.96	1.75	**1.17**
H. habilis	3.45	**2.63**	3.40
H. erectus	**2.81**	2.91	3.59
H. ergaster	**1.98**	3.57	4.22
H. neanderthalensis	**1.19**	4.54	5.19
H. floresiensis	**1.77**	4.97	5.72

The figure in bold in each row is the shortest distance

Collard's (1999) definition of the genus, the available data on its adaptive strategy clearly suggest that there is a problem. Given that some of its adaptive characteristics are consistent with those seen in the other species assigned to genus *Homo* by Wood and Collard (1999) while others are not (Table 5), either Wood and Collard's (1999) approach to defining *Homo* needs to be amended, or *H. floresiensis* needs to be assigned to a different genus. In our view, the latter course of action is preferable until the phylogenetic relationships and adaptive strategy of the species have been more fully evaluated.

There also have been developments in two areas that impact Wood and Collard's (1999) conclusions regarding the adaptive strategies of *H. erectus*, *H. ergaster*, *H. habilis*, *H. heidelbergensis*, *H. neanderthalensis*, *H. rudolfensis*, and *H. sapiens*. One of these concerns the life history strategies of the fossil species. The period of maturation of *H. sapiens* is nearly twice as long as those of the *G. gorilla* and *P. troglodytes* (Dean et al. 1986; Smith 1994). This extended ontogeny has been linked with the transmission of the numerous additional learned behaviors that

Table 5 Summary of results of adaptive strategy analyses

Taxon	1	2	3	4	5	6
H. rudolfensis	?	?	?	A	A	A
H. habilis	A	A	A	A	A	A
H. ergaster	H	H	H	H	A	A
H. erectus	H	?	H	H	A	I
H. heidelbergensis	H	?	H	H	?	A
H. neanderthalensis	H	H	H	H	H	H
H. floresiensis	A	A	A	H	?	A

This is a revised version of Wood and Collard (1999)'s Table 7. *1* body size, *2* body shape, *3* locomotion, *4* jaws and teeth, *5* development, *6* brain size, *H* modern human-like, *A* australopith-like, *I* Intermediate

modern humans exhibit compared to the African apes. Wood and Collard's (1999) review of the literature led them to conclude that the developmental schedules of *H. ergaster* and *H. neanderthalensis* were more similar, if not identical, to that of *H. sapiens*, whereas the developmental schedules of *H. habilis* and *H. rudolfensis* were more like those of living chimpanzees and gorillas. Wood and Collard (1999) did not discuss the developmental schedules of *H. erectus* and *H. heidelbergensis* because at the time their paper went to press no comparative analysis of hominin development had included specimens of these species.

It is now clear that Wood and Collard's (1999) conclusions regarding the life history strategies of the fossil *Homo* species need to be modified. While there are differences between what can be determined about the growth trajectory of Neanderthals and the growth trajectory of modern humans (Thompson and Nelson 2000; Ramirez Rozzi and Bermudez de Castro 2004; Smith et al. 2010), the developmental schedule of *H. neanderthalensis* appears to have been more modern human-like than ape-like (Dean et al. 2001). In contrast, the developmental schedules of *H. habilis* and *H. rudolfensis* appear to have been more ape-like than modern human-like (Dean et al. 2001). However, the hypothesis that the maturation period of *H. ergaster* was modern human-like no longer appears tenable. Dean et al.'s (2001) comparative analysis of fossil hominin dental incremental markings suggests that while the pattern of development in *H. ergaster* is similar to the pattern of development in *H. sapiens*, the rate at which *H. ergaster* developed was more ape-like than modern human-like. In addition to altering the assessment of the developmental schedule of *H. ergaster*, work published since Wood and Collard's (1999) study appeared has shed light on the life history strategy of *H. erectus*. Dean et al. (2001) included a specimen assigned to *H. erectus* in their study. They concluded from this specimen, Sangiran S7-37, that *H. erectus* reached maturity relatively rapidly. *Homo erectus* was also found to have had an ape-like pattern of brain growth in a study reported by Coqueugniot et al. (2004) in which the infant *H. erectus* specimen from Java, Perning 1, was compared with a sample of modern humans and chimpanzees. A number of recent studies have examined development in *H. heidelbergensis* (Bermudez de Castro and Rosas 2001; Ramirez Rozzi and

Bermudez de Castro 2004; Bermudez de Castro *et al*. 2003). Unfortunately, these studies have been carried out in such a way that it is difficult to assess with confidence whether the developmental schedule of *H. heidelbergensis* was more like that of *H. sapiens* than those of the great apes, or vice versa. Nonetheless, the fact that Ramirez Rozzi and Bermudez de Castro (2004) find enamel extension rates to be slower in *H. heidelbergensis* than in Neanderthals suggests that *H. heidelbergensis* was more modern human-like than ape-like in its developmental schedule. Thus, it now appears that the developmental schedules of *H. heidelbergensis* and *H. neanderthalensis* were more similar to the developmental schedule of *H. sapiens* than to those of chimpanzees and gorillas, whereas the developmental schedules of *H. erectus*, *H. ergaster*, *H. habilis*, *and H. rudolfensis* were more like those of chimpanzees and gorillas.

The other area in which there have been developments that affect Wood and Collard's (1999) conclusions regarding the adaptive strategies of the species conventionally assigned to genus *Homo* is locomotor behavior. Their case for removing *H. habilis* from genus *Homo* was based, in part, on the fact that they considered it to have been a facultative biped like the australopiths rather than an obligate biped like *H. ergaster*, *H. erectus*, *H. heidelbergensis*, *H. neanderthalensis*, and *H. sapiens*. The locomotor behavior of *H. rudolfensis* was not considered because in the absence of an associated skeleton nothing is known for certain about its postcranial morphology. Wood and Collard (1999) cited three lines of evidence in support of their claim about H. habilis. One of these was the morphology of the hand bones associated with OH 7, the type specimen of the species, which have been interpreted as being consistent with an apelike climbing ability (Susman and Creel 1979). Another was the configuration of the semi-circular canals in the southern African *H. habilis* specimen Stw 53. This is so markedly different from the configuration in *H. sapiens* (Spoor et al. 1994) that it is likely the two taxa had different balancing requirements. The third line of evidence Wood and Collard (1999) cited in support of the hypothesis that *H. habilis* was a facultative biped was the limb proportions of the two associated skeletons, OH 62 and KNM-ER 3735, that have been assigned to *H. habilis*. These had been reconstructed as being more primitive than those of *Au. afarensis* (Hartwig-Scherer and Martin 1991). Humerus length is similar in modern humans and living chimpanzees, but the former have shorter forearms than the latter. They also have markedly longer femurs. These differences in limb proportions are thought to be related to the contrasting locomotor strategies of the two species: the long femurs of modern humans being adaptive for bipedalism, and the long forearms of living chimpanzees being adaptive for climbing. The available evidence pertaining to limb proportions in australopiths suggests that their forearms were comparatively long while their femora were intermediate in length between those of humans and chimpanzees. This is consistent with the hypothesis that australopiths combined facultative terrestrial bipedalism with proficient climbing. Thus, Hartwig-Scherer and Martin's (1991) finding that the limb proportions of OH 62 and KNM-ER 3735 were more primitive than those of *Au. afarensis* reinforced the hypothesis that *H. habilis* was a facultative biped.

Since Wood and Collard's (1999) study went to press, a number of analyses have been published that challenge the hypothesis that the limb proportions of *H. habilis* were more primitive than those of the australopiths. For example, in 2002 Brian Richmond, Leslie Aiello and Bernard Wood reported the results of a randomization-based study designed to examine the significance of the limb proportion differences among several early hominins, including OH 62 and the only *Au. afarensis* associated skeleton, AL 288-1. They found that the limb proportions of OH 62 are not statistically significantly different from those of AL 288-1. Thus their analyses did not support the hypothesis. More recently, Reno et al. (2005) have argued that the humerofemoral index of OH 62 cannot be calculated because the portion of femur it retains – the proximal part – is a poor predictor of maximum femur length. This claim is supported by an analysis of the relationship between proximal and maximum femur length in extant hominoids, which suggests that the two lengths are not significantly correlated. Although some researchers have taken issue with the methods and assumptions used by Reno et al. (2005), the lack of association between proximal and maximum femur length in their sample of humans and apes certainly suggests that current estimates of the length of OH 62's femur or of its humerofemoral index must be treated with caution. Thus, there is no longer any support for the claim that the limb proportions of OH 62 are more primitive than those of the australopiths; the most that can be said is that they are australopith-like.

The developments that have taken place over the last few years in relation to fossil hominin life histories and locomotor abilities have certainly challenged Wood and Collard's (1999) conclusions regarding the adaptive strategies of some of the species conventionally assigned to genus *Homo*. Most notably, they suggest that *H. erectus* and *H. ergaster* were less modern human-like than Wood and Collard's (1999) analyses suggested. However, on balance, the available evidence still suggests that the adaptive strategies of *H. habilis* and *H. rudolfensis* were different from those operated by *H. erectus*, *H. ergaster*, *H. heidelbergensis*, *H. neanderthalensis* and *H. sapiens* (Table 5). Taken together with the results of the phylogenetic studies that have been published in the last 7 years, this suggests that Wood and Collard's (1999) proposal to remove *H. habilis* and *H. rudolfensis* from *Homo* and assign them to a different genus or pair of genera remains valid.

Conclusion

There is a widespread belief that hominin systematics is arcane and irrelevant, but in our view this notion is ill-founded. Sound taxonomic units are a prerequisite for progress in evolutionary biology (Crowson 1970; Panchen 1992). Thus, *more* attention should be paid to the systematics of the hominins, not less. With this in mind, we hope that the points we have made in this chapter stimulate further work on the definition and composition of the genus *Homo*. In particular, there is a pressing need for Mayr's (1950) and Cela-Conde and Altaba's (2002) approaches to defining genera to be operationalized satisfactorily. We also badly need reliable information about both the phylogenetic relationships of the early *Homo* species and their postcranial morphology, especially as it relates to locomotion. Lastly, it would be helpful for the systematic comparative approach to analyzing dental development employed by Dean et al. (2001) to be extended to the fossils assigned to *H. heidelbergensis* and to the taxon that, for the time being at least, is referred to as *H. floresiensis*.

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Cross-References

- ▶ Analyzing Hominin Phylogeny: Cladistic Approach
- ▶ Defining Hominidae
- ▶ Defining *Homo erectus*
- ▶ Estimation of Basic Life History Data of Fossil Hominoids
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Later Middle Pleistocene *Homo*
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Bipedal Locomotion
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- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Quantitative Approaches to Phylogenetics
- ▶ Role of Environmental Stimuli in Hominid Origins
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Earliest Putative *Homo* Fossils
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Species and Diversity of Australopiths

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The Earliest Putative *Homo* Fossils

Friedemann Schrenk, Ottmar Kullmer, and Timothy Bromage

Contents

Abstract

The earliest fossil remains of the genus *Homo* have been discovered in eastern, southeastern, and southern Africa. The sample comprises about 200 skeletal fragments attributable to about 40 individuals and assigned to two species: *Homo rudolfensis* (2.5–1.8 Ma) showing a combination of primitive dentition with *Homo*-like locomotion and *Homo habilis* (2.1–1.5 Ma) exhibiting a progressive reduction of tooth roots but resembling great apes rather than humans in the postcranial skeleton. Another significant difference between early *Homo* and the australopithecines is brain size, which was larger in early *Homo* than in *Australopithecus* but smaller than in *Homo erectus*. Endocasts of *H. habilis* from

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F. Schrenk (✉) • O. Kullmer
Department of Paleoanthropology and Messel Research, Senckenberg Research Institute and Natural History Museum, Frankfurt, Germany
e-mail: schrenk@bio.uni-frankfurt.de; ottmar.kullmer@senckenberg.de

T. Bromage
Department of Biomaterials and Biomimetics, New York University, College of Dentistry, New York, NY, USA
e-mail: tim.bromage@nyu.edu

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Olduvai Gorge and Koobi Fora reveal a number of distinctive features, some of which are recognized as *Homo* autapomorphies. Differences in tooth wear between *H. rudolfensis*, with megadont teeth and more horizontal tooth abrasion, and *H. habilis*, with more gracile molars and higher relief in worn teeth, indicate significant differences in diet and ecology of early *Homo* species. The origin of the genus *Homo* coincided with the onset of material culture. Between ca. 2.8 and 2.5 Ma, extensive open habitats comprising more arid-tolerant vegetation developed in Africa. The selective pressures of this habitat change resulted in the increased survival of more megadont species varieties. Megadonty allowed these species to feed on harder open woodland-open savannah food items (chapter "▶ Dental Adaptations of African Apes," Vol. 2) resulting in the phyletic splitting of *Australopithecus afarensis* into *Paranthropus* and *Homo* lineages by ca. 2.5 Ma. An evolutionary scenario that complies with both the Habitat Theory and early hominid biogeography is provided. It delineates the association between faunal turnover and climate change and suggests a single origin for the *Paranthropus* lineage but separate origins for *H. rudolfensis* and *H. habilis* from *A. afarensis*, *A. africanus*, or *A. sediba* ancestors, respectively.

Introduction

The search for the roots of the genus *Homo* is of particular interest in the field of paleoanthropology. The taxonomic determination of the earliest putative *Homo* fossils provides the basis for the definition of the taxon *Homo* to which all modern humans belong.

Carolus Linnaeus (1758) established the genus *Homo* in the tenth revision of his *Systema Naturae* (chapter "▶ Historical Overview of Paleoanthropological Research," Vol. 1). In his opinion, *Homo* subsumed six groups: *H. sylvestris*, *H. troglodytes* (a mixture of orangutan and myths), *H. sapiens*, and four geographical variants from Africa, America, Asia, and Europe. In the two centuries that followed, *H. neanderthalensis* (King 1864), *H. heidelbergensis* (Schoetensack 1908), *H. erectus* (Dubois 1892; Mayr 1944), *H. habilis* (Leakey et al. 1964), *H. ergaster* (Groves and Mazák 1975), *H. rudolfensis* (Alexeev 1986), *H. antecessor* (Bermudez de Castro et al. 1997), and others were all included in the genus *Homo* (overview in Henke and Hardt 2011).

The history of research, the order of discoveries, and the existing paradigms heavily influence the formation and change in the interpretations of human evolution. This holds true especially regarding ideas on the origin of the genus *Homo* since the 1960s. Debates on the attribution of fossil specimens and the definition of the genus *Homo* continue, and up to date, the taxonomic interpretation of earliest *Homo* is highly controversial (Wood and Collard 2001; Wood and Lonergan 2008; Lordkipanidze et al. 2013).

Opinions differ regarding the number of species and also the specimens included in the genus. Some even assign all putative *Homo* specimens to living humans

(*H. sapiens*). In practical terms, species names in paleoanthropology are labels rather than natural species, and the taxonomic determination of fossils is more or less a question of the philosophy followed by the authors. There are both theoretical and practical reasons to erect taxa, as chronospecies for time equivalent appearance or morphospecies for a complex of shared anatomical features, and in the worst case, there are political reasons for the allocation of species (chapters "▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms," "▶ Species Concepts and Speciation: Facts and Fantasies," Vol. 1, "▶ Defining Hominidae," "▶ *Homo ergaster* and Its Contemporaries," and "▶ Defining the Genus *Homo*," Vol. 3).

Fossil Evidence

Early research on the origin of the genus *Homo* is closely related to the African fieldwork of Louis S. B. Leakey (1903–1972). He strongly believed in Africa as the cradle of humankind and in 1932 discovered the first evidence of early *Homo* at Kanam (Kenya), east of Lake Victoria – a specimen, which today is attributed to *H. erectus*. He also undertook archaeological surveys in Olduvai Gorge, Tanzania (Fig. 1), where later he discovered early pebble tools in Bed I (ca. 1.8 Ma) – remains of what he termed the "Oldowan" industry. The search for the artifact creator led to the discovery of robust australopithecine remains (*Zinjanthropus boisei*) (Leakey 1959). However, due to its small brain size, this specimen Olduvai Hominid 5 (OH 5) was not a convincing candidate for the first toolmaker.

A year later, Louis' son Jonathan Leakey discovered two fragments of a relatively gracile skull, a lower jaw (Fig. 2), and several hand bones of OH 7 (Leakey 1961), deriving from the same stratigraphic level (Bed I) at Olduvai. Brain volume was estimated at around 680 cm^3, a significantly higher value than in robust australopithecines. Consequently, this fossil was interpreted as representing a progressive hominid type of unknown species affiliation. Later Leakey et al. (1964) decided on the new species *H. habilis*. Raymond A. Dart, the founder of modern paleoanthropology in Africa, who in 1925 had introduced the genus *Australopithecus*, had suggested this name to them (chapter "▶ The Species and Diversity of Australopiths," Vol. 3). The Latin term "habilis" means "handy, skillful, able": finally, the producer of the Oldowan culture seemed to have been identified.

Apart from OH 7, the species description of *H. habilis* included skull fragments and teeth (OH 4 and OH 6), part of an adult foot (OH 8), and the incomplete skull of an adolescent (OH 13). Further, Leakey et al. (1964) referred a collection of juvenile cranial pieces (OH 14) and the fragmented cranial vault and dentition (OH 16) of a young adult to the new species.

Since then, numerous additional fossils assigned to *H. habilis* have been discovered at Olduvai Gorge: nine fragmentary skulls, four mandible fragments, 19 teeth, and eight postcranial fragments. Among these fragments was the squashed skull OH 24 ("Twiggy"), which was found in 1968. In 1986, a partial female skeleton

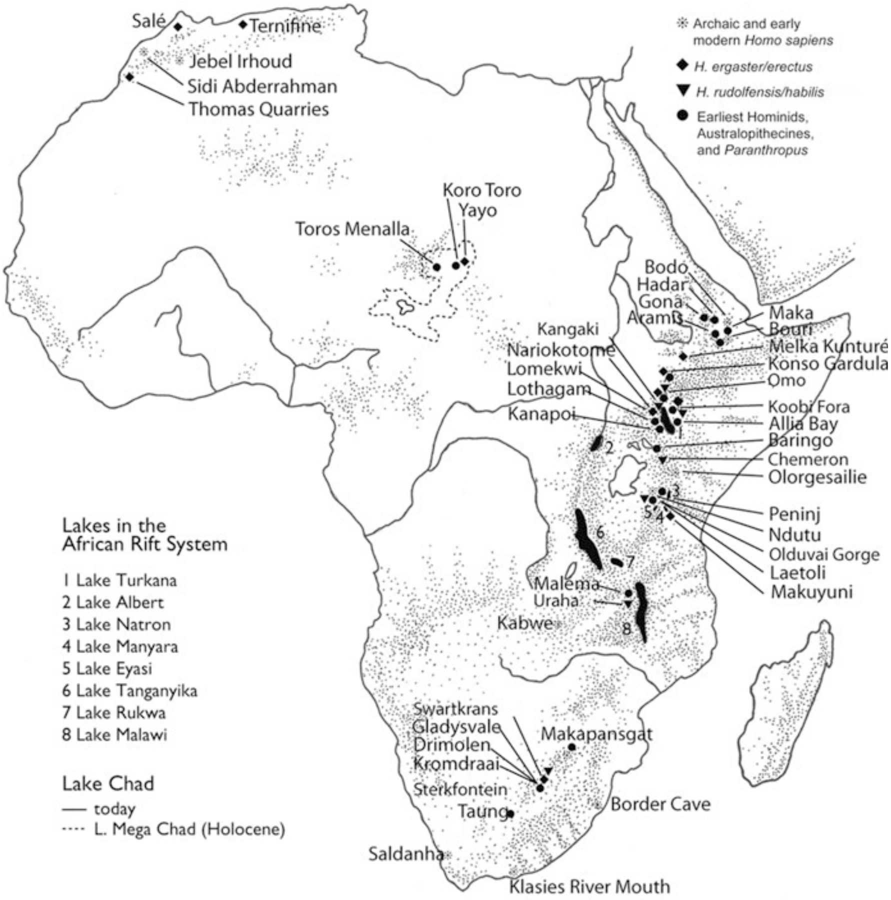
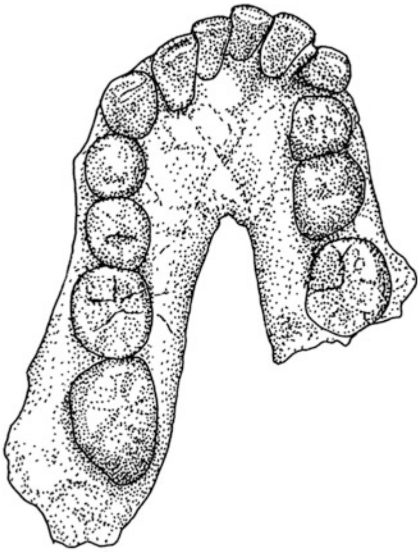


Fig. 1 African early hominid sites. *Homo rudolfensis* and *Homo habilis* sites (▼)

(OH 62) was assembled from a number of fragments (Johanson et al. 1987). This specimen showed that *H. habilis* was fully bipedal and had a brain larger than all australopithecines. For many years, the *H. habilis* remains from Olduvai Gorge were seen as the most important early *Homo* specimens and consequently played the leading role in most hypotheses regarding the origin of genus *Homo* (chapters "▶ Analyzing Hominin Phylogeny: Cladistic Approach," "▶ Defining the Genus *Homo*," Vol. 3).

Leakey et al. (1964) originally discussed cranial and mandibular traits to distinguish the *Homo* specimens of Olduvai from australopiths and *H. erectus*. Maxillary and mandibular size is smaller than in *Australopithecus* and tends in size to *H. erectus* and *H. sapiens*. The surface of the skull shows slight to strong muscular markings, and the parietal curvature in the sagittal plane varies from slight to moderate. The frontal bone is more vertical and the torus supraorbitalis is less

Fig. 2 Type specimen of *Homo habilis*: mandible OH 7, Olduvai Gorge, Tanzania



developed than in australopithecines. In the occipital region, the relatively open-angled external sagittal curvature differs markedly from *Australopithecus*.

In 1970 the picture of earliest *Homo* began to change significantly with the success of the Koobi Fora Research Project in northern Kenya led by Richard Leakey, Louis' son. In just a few years on the eastern shores of Lake Turkana, his team recovered nine skulls, ten mandibles, six isolated teeth, and five postcranial fragments (Leakey 1973a, b). Originally, all the early *Homo* finds from East Turkana, with an age similar to those from Olduvai (1.9–1.8 Ma), were interpreted as bearing similarities to *H. habilis* – then the only early species of *Homo* known. One cranial fragment from the Nachukui Formation on the western shores of Lake Turkana was also assigned to *H. habilis*. However, two of the best preserved skulls from Koobi Fora (KNM-ER 1470, Fig. 3a; KNM-ER 1813, Fig. 3b) later gave rise to an extended debate among researchers about the heterogeneity of the *H. habilis* hypodigm and finally led to the recognition of a new species, *H. rudolfensis* (Alexeev 1986; Wood 1992).

In the 1970s a large number of isolated *Homo* teeth were discovered north of Koobi Fora, near the Omo River in southern Ethiopia, in Members G and H of the Shungura Formation. From these it became clear that the origin of the genus *Homo* extended well beyond 2 Ma. In 1965 a temporal bone was discovered by John Martyn at Chemeron, Kenya, and nearly two decades later, it was described by Hill et al. (1992) as a very early member of the genus *Homo*, dated to around 2.4 Ma.

In 1976, an early *Homo* fossil was found at Sterkfontein, South Africa (Stw 53), that belonged neither to *H. erectus* nor to *Australopithecus* (Hughes and Tobias 1977). A partial facial skull (SK 847 from Swartkrans), assembled from several fragments, originally attributed to a different species, is further evidence for *H. habilis*, which probably migrated into southern Africa around

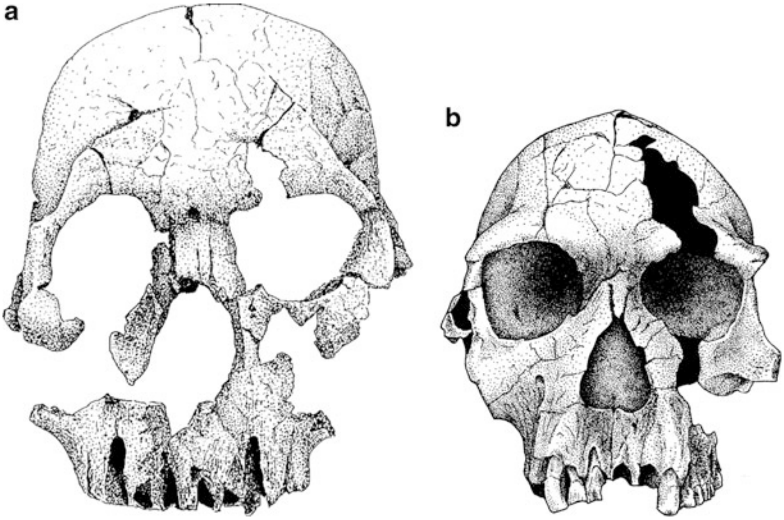


Fig. 3 (**a**) (*left*) KNM-ER 1470 from Koobi Fora, Kenya (ca. 1.9 Ma) *Homo rudolfensis*. (**b**) (*right*) KNM-ER 1813 from Koobi Fora, Kenya (ca. 1.9 Ma) *Homo habilis*. (Scale ca. 1 : 2) (Drawing: Claudia Schnubel)

2 Ma (see below). A new species, *Homo gautengensis*, was established by Curnoe 2010, encompassing finds from Sterkfontein, which earlier had been classified as *Homo habilis* (Curnoe 2010).

The geographical gap between the southern and eastern African early hominid sites was filled in the early 1990s through discoveries in the "Hominid Corridor" of the northern Malawi Rift (Schrenk et al. 1993; Bromage and Schrenk 1995). In 1992, at Uraha, the Hominid Corridor Research Project (HCRP) recovered a mandibular corpus, UR 501 (Fig. 4), containing third and fourth premolars and first and second molars in variable states of preservation (Schrenk et al. 1993). Many absolute and relative measures defining molar and premolar crown shape indices, relative cusp areas, fissure patterns, and enamel microanatomical features, as well as overall crown morphology, are within the sample range of early *Homo*, although some may also be subsumed within the limits of variation represented by *Australopithecus* (*A. africanus* and *A. afarensis*). However, UR 501 has absolutely large molar crown areas, relative expansion of the P_3 talonid, platelike P_3 and P_4 roots, and some enamel microanatomical features correspond more closely to the *Paranthropus* condition. UR 501 corresponds closely to the subset of Late Pliocene fossils from East Turkana, Kenya, which have relatively large brains and robust jaws and teeth and based on the above were assigned to *H. rudolfensis* by Alexeev (1986) and Wood (1992). UR 501 was also referred to this group (Bromage et al. 1995). This Malawi specimen has been dated by biostratigraphic correlation of suid material with well-dated sites in southern Ethiopia (Omo Shungura) and northern Kenya (Koobi Fora), indicating an age of about 2.3–2.5 Ma (Kullmer 2008), whereas most early *Homo* fossils are around 2 Myr old.

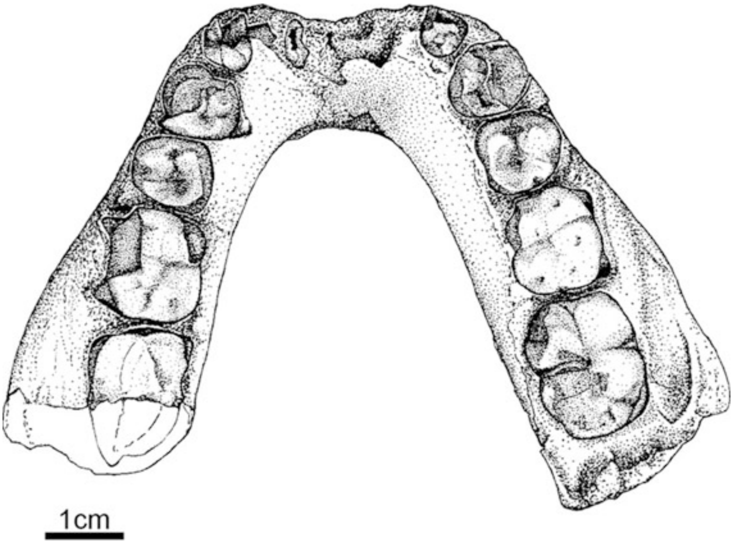


Fig. 4 UR 501 from the Chiwondo Beds, northern Malawi (ca. 2.5–2.3 Ma), *Homo rudolfensis* (Drawing: Claudia Schnubel)

It is important to note that the appearance of earliest *Homo* is contemporaneous with the origin of hyperrobust australopithecines (*Paranthropus*) (chapters "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1 and "▶ Origins of Homininae and Putative Selection Pressures Acting on the Early Hominins," Vol. 3). The earliest evidence for this co-existence is based on further hominid discoveries in the Chiwondo Beds of northern Malawi (Kullmer et al. 1999, 2011). A maxillary fragment (RC 911) preserves part of the left alveolar process, with badly damaged M^1 crown and fragmentary M^2 crown. Size, morphology, and abrasion occlusal pattern on the surface suggest that RC 911 should be assigned to *Paranthropus boisei* (Kullmer et al. 1999; Alt et al. 2000).

The biogeographic significance of these Malawi Rift hominids lay in their association with the eastern African endemic faunal group. The associated bovid and suid faunas show a small amount of overlap with southern African animals and a greater overlap with eastern African faunal elements. Biogeographic variation in the Malawi Rift may be linked to habitat changes occurring due to climate shifts, with maximum change occurring around 2.5 Ma.

Changing Taxonomy

Hominid fossils have been assigned to the genus *Homo* if they fulfilled four main perceived criteria (Keith 1948; Tobias 1991; Wood and Collard 2001): a brain size above 600 cm^3, putative ability for speech and toolmaking, and an opposable

Table 1 Significant morphological differences between *H. habilis* and *H. rudolfensis*

	Homo habilis sensu stricto	*Homo rudolfensis*
Skull and teeth		
Absolute brain size (cm^3)	An average volume of 610	An average volume of 650–675
Overall cranial vault morphology	Enlarged occipital contribution to the sagittal arc	Primitive condition
Endocranial morphology	Primitive sulcal pattern	Frontal lobe asymmetry
Suture pattern	Complex	Simple
Frontal	Incipient supraorbital torus	Torus absent
Parietal	Coronal > sagittal chord	Primitive condition
Face overall	Upper face > midface breadth	Midface > upperface breadth
Nose	Margins sharp and everted; evident nasal sill	Less everted margins; no nasal sill
Malar surface	Vertical or near vertical	Anteriorly inclined
Palate	Foreshortened	Large
Upper teeth	Probably two-rooted premolars	Premolars three rooted; absolutely and relatively large anterior teeth
Mandibular fossa	Relatively deep	Shallow
Foramen magnum	Orientation variable	Anteriorly inclined
Mandibular corpus	Moderate relief on external surface; rounded base	Marked relief on external surface; everted base
Lower teeth	Buccolingually narrowed; postcanine crowns; reduced talonid on P_4; M_3 reduction; mostly single-rooted mandibular premolars	Broad postcanine crowns; relatively large P_4 talonid; no M_3 reduction; twin, platelike P_4 roots, and bifid, or even twin, platelike P_3 roots
Postcranium		
Limb proportions	Apelike	?
Forelimb robusticity	Apelike	?
Hand	Mosaic of apelike and modern humanlike features	?
Hindfoot	Retains climbing adaptations	Later *Homo*-like
Femur	Australopithecine-like	Later *Homo*-like

After Wood (1992)

pollux. To date, the hypodigm of earliest *Homo* attributed to *H. habilis sensu stricto* and *H. rudolfensis* contains about 200 skeletal fragments attributable to about 40 individuals (Tables 1 and 2). Despite or maybe due to the large number of specimens, the taxonomic interpretation of earliest *Homo* is highly controversial (e.g., Wood 2000).

Table 2 Fossil remains of *Homo habilis sensu stricto*

Homo habilis (better-preserved specimens in bold)

Sites	Skulls and crania	Mandibles	Isolated teeth	Postcranial
Olduvai (OH)	6, **7**, **13**, 14, **16**, **24**, 52, 62	**7**, **13**, 37, 62	4, 6, 15, **16**, 17, 21, 27, 31, 32, **39**, 40, 41, 42, 44, 45, 46, 47, 55, 56	**7**, **8**, 10, **35**, 43, 48, 49, 50, **62**
Koobi Fora (KNM-ER)	807, 1478, **1805**, **1813**, 3735	**1501**, 1502, 1506, **1805**, 3734	808, 809, 1462, 1480, 1508, 1814	**813**, **1472**, **1481**, **3228**, 3735
Omo	**L894-1**	**Omo 222-2744**	L28-31; L398-573, 1699; Omo 33-3282, Omo 47-47; Omo 74-18; Omo 123-5495; Omo 166-781; Omo K7-19; Omo SH1-17; P933-1	
West Turkana	Kangaki I site (w/o number)	–	–	–
Sterkfontein	**Stw 53**, SE 255, 1508, 1579, 1937, 2396; Sts 19	–	–	–
Swartkrans	SK 847 (?)	–	–	–

Originally, the interpretation of the early *Homo* hand as "modern" (Leakey et al. 1964) supported the view of *H. habilis* as an early but "able" human as opposed to the rather "clumsy" australopithecines. However, later skeletal finds at Olduvai Gorge (OH 62) (Johanson et al. 1987) demonstrated that the postcranial skeleton of *H. habilis* indeed resembled *Australopithecus africanus* rather than *Homo*. Yet the most distinctive character of *H. habilis* remains its relatively and absolutely higher brain volume compared to that of *Australopithecus*. The forehead of *H. habilis* is more vertical and a weak supraorbital torus is present. Whereas the morphological characters are quite uniform in the Olduvai sample, the discussion started to heat up mainly over two very distinct fragmentary skulls from Koobi Fora: KNM-ER 1470 (Fig. 3a) (Leakey 1973a) and KNM-ER 1813 (Fig. 3b) (Leakey 1973b).

In a comprehensive character analysis of all available putative *H. habilis* fossils from Koobi Fora, Wood (1991) concluded that the variability exhibited by the sample was not only the result of sexual dimorphism, as was suspected at the time, but that highly significant differences exist throughout the entire skeleton. There is a mosaic of *Australopithecus* and *Homo* characters in both early species: Whereas *H. rudolfensis* exhibits a combination of ancestral dentition with *Homo*-like

Table 3 Fossil remains of *Homo rudolfensis*

Homo rudolfensis (better-preserved specimens in bold)				
Sites	Skulls and crania	Mandibles	Isolated Teeth	Postcranial
Koobi Fora (KNM-ER)	**1470**, **1590**, **3732**, 3891	819, **1482**, 1483, 1801, **1802**	–	–
Chemeron	KNM-BC 1	–	–	–
Omo		**Omo 75-14**	? L7-279; L26-1 g; L28-30, L628-10; Omo 29-43; Omo 33-740, 5495, 5496; Omo 75i-1255; Omo 75 s-15, 16; Omo 177-4525; Omo 195-1630	
West Turkana	Lokalalei? WT 42718	–	–	–
Uraha (UR)	–	**501**	1106	–

locomotion, *H. habilis* shows a progressive reduction of tooth roots and resembles great apes rather than humans postcranially.

Based on the work of Wood (1991) and subsequent re-evaluation of fossils, it is evident that two distinct types can be separated. Whereas one group, represented by KNM-ER 1813, follows the original description of *H. habilis* from Olduvai Gorge, a new group is represented by KNM-ER 1470, for which no comparison existed in Olduvai at the time. Although the subsequent find of OH 65 at Olduvai (Blumenschine et al. 2003) showed a mixture of *H. habilis sensu stricto* and KNM-ER 1470 features, it is still a valid conclusion that about half the early *Homo* material from Koobi Fora belongs to *H. habilis sensu stricto*, with an age of 2.1–1.5 Ma, which includes also specimens from Koobi Fora, West Turkana, Omo, Olduvai Gorge, and southern Africa (Table 2). Hominid remains from Ubeidiya in Israel (Leakey et al. 1964) and *Meganthropus palaeojavanicus* from Java, Indonesia, which at one stage were tentatively assigned to *H. habilis* (Tobias and von Koenigswald 1964), are not considered as such today.

The Koobi Fora early *Homo* material not assigned to *H. habilis* is allocated to the more recently named species *H. rudolfensis*, with an age of 2.5–1.8 Ma, which also includes specimens from Chemeron, West Turkana (Prat et al. 2005), and Omo (Suwa et al. 1996; Ramirez Rozzi 1997), as well as northern Malawi (Schrenk et al. 1993) (Table 3).

The species name *rudolfensis* was coined by Russian paleontologist Valerij Pavlovič Alexeev, who in 1986 described KNM-ER 1470 as "*Pithecanthropus rudolfensis*," after Lake Rudolf, the name of Lake Turkana prior to Kenyan independence in 1963.

Postcranial Skeleton

The postcranial skeleton of *H. habilis* was characterized by Leakey et al. (1964) using a number of characteristics: the clavicle resembles that of *H. sapiens*, the hand shows broad terminal phalanges, and capitate and MCP articulations also resemble *H. sapiens*, but differ in respect to the scaphoid and trapezium, attachments of the superficial flexor tendons, and the robusticity and curvature of the phalanges. The foot bones resemble *H. sapiens* in the stout and adducted hallux and well-defined foot arches, but differ in shape of the talar trochlea surface and the relatively robust third metatarsal.

All these features indicate an affinity toward *H. sapiens* and underline that the early postcranial material from Olduvai seems to be different from that of the australopiths. Functional implications based on more detailed descriptions of the foot (OH 8, OH 10) and leg (OH 35), both of which are probably from the same individual (Stern and Susman 1983), were generally more cautious (Wood 1992). According to Stern and Susman (1983), *H. habilis* had not reached the characteristic bipedal gait of *H. sapiens*, since the functional morphology of the knee joint was not well adapted for striding. Further analysis of the OH 8 foot demonstrated that some features, common in nonhuman hominoids, are also present in the foot bones (Lewis 1989). As more postcranial material was uncovered at Koobi Fora, interpretation of hind limb function of early *Homo* became more complex. However, some specimens, such as the femur KNM-ER-1472A and the talus KNM-ER-813, may belong to *H. erectus* or *H. ergaster* rather than to *H. habilis* (Tobias 1991). Although the partial skeleton OH 62 from Olduvai Gorge was interpreted as evidence for fully upright human bipedal locomotion, Haeusler and McHenry (2004) demonstrated that there is little evidence in support of ancestral body proportions with short legs and long arms in *H. habilis*. Their results suggest that it is more likely that earliest *Homo* possessed an elongation of the legs relative to *A. africanus* and *A. afarensis*, whereas long forearms were still retained (Johanson et al. 1987). With its upper-to-lower limb shaft length proportions, OH 62 falls within the upper range of modern humans and the lower range of chimpanzees due to the partial overlap between these taxa at small body sizes. KNM-ER 3735, the larger-bodied early *Homo* from Koobi Fora, falls well outside the chimpanzee range and reflects the average proportions of modern humans. Comparison of the Koobi Fora and Hadar postcranial remains has led to the interpretation that *H. habilis* did probably possess a modern pattern of limb shaft proportions, and the body proportions of OH 62 are in agreement with other available evidence of *H. habilis* postcranial material (Johanson et al. 1987), but Jungers (2009) judges OH 62 interlimb proportions as indeterminate. The change in the proportions of limb length toward the development of long legs may be indicative of long-distance terrestrial running in early *Homo* and probably implies a shift in hominid ecology (Bramble and Lieberman 2004).

Brain and Language

A significant difference between early *Homo* and australopiths exists in brain size, which was larger in early *Homo* than in *Australopithecus* but smaller than *H. erectus*. Endocasts of *H. habilis* from Olduvai and Koobi Fora reveal a number of distinctive features, some of which are recognized as autapomorphies of the genus *Homo*. Tobias (1987) defined the principal morphological trait to distinguish *H. habilis* from *Australopithecus* as a larger mean endocranial capacity in the former (640 cm^3) than in *A. africanus* (441 cm^3), *A. boisei* (513 cm^3), and *A. robustus* (530 cm^3) (chapters "▶ The Evolution of the Hominid Brain," Vol. 3 and "▶ The Evolution of Speech and Language," Vol. 1). This suggests that the evolutionary trend toward brain expansion was already well under way more than 2 Ma. The *H. habilis* mean (640 cm^3) is close to the lower limit (647 cm^3) of the 95 % population range of *H. erectus* but well above the upper limit of the *A. africanus* range (492 cm^3). The brain capacity of the *H. rudolfensis* type specimen, originally reconstructed to give 752 cm^3, is larger than the known range for *H. habilis* from Olduvai Gorge and Koobi Fora and falls within the lower range of *H. erectus*. However, the relationship between prognathism and cranial capacity in primates results in an estimate of KNM-ER 1470 cranial capacity of 625 cm^3 (1 SD = 49 cm^3), and together with other considerations, a ca. 700 cm^3 estimate is more realistic (Bromage et al. 2008). This revision is not inconsistent with other Late Pliocene *Homo* prior to the appearance of Early Pleistocene *Homo erectus/ergaster* (Holloway 1996).

A prominent feature of the *H. habilis* brain is the bilateral transverse expansion of the cerebrum, especially in the frontal and parieto-occipital areas, and a posterior heightening. The increased bulk of cerebral frontal and parietal lobes and the sulcal and gyral patterns of the lateral frontal lobe have been interpreted as derived features for the genus *Homo* (Tobias 1987). The *H. habilis* brain showed a well-developed left superior parietal lobule and a prominent development of the inferior parietal lobule.

The endocast of KNM-ER 1470 shows a left frontal lobe sulcal pattern that is associated with Broca's area in living people (Falk 1987), a finding that has led to the conclusion that *H. rudolfensis* may have been capable of speech. This conclusion is in accordance with Holloway's observation of a pronounced left-occipital-right-frontal petalia pattern in the KNM-ER-1470 endocast that may indicate functional cortical asymmetry (Holloway 1983). Surprising corroborative evidence has been provided by Toth's analyses (chapters "▶ Overview of Paleolithic Archaeology," Vol. 3 and "▶ Modeling the Past: Archaeology," Vol. 1) of stone flakes, which indicate that hominids were predominantly right-handed by 2 Ma (Toth 1985). Adjacent areas in the left frontal lobe control the speech organs and the right hand. Tobias (1991) stated that *H. habilis* is the earliest hominid to show prominent enlargement of Broca's and Wernicke's areas. If so, the same should be seen in *H. rudolfensis*. *Australopithecus* endocasts show Broca's area, but not Wernicke's region, while anthropoid apes display neither of the two. The prominent development of the two speech areas may thus be seen as an important autapomorphy of the genus *Homo* (Tobias 1991). Even if *H. habilis* and

H. rudolfensis possessed the neurological bases of speech, there is no evidence that either of them used spoken language. The areas of the brain that control spoken (chapter "▶ The Evolution of the Hominid Brain," Vol. 3) communication probably manifested themselves only when brain enlargement occurred and marked encephalization started.

Material Culture and Food Processing

Around 2.5 Ma, simultaneously with an increase in drier and harder food stuffs due to increasing aridity in eastern Africa (de Menocal 2004), there occurred the first hyperrobust australopithecines (*Paranthropus*) and the first specimens identified as genus *Homo* in the fossil record (Bromage et al. 1995). This demonstrates an evolutionary alternative to the massive masticationary system of *Paranthropus*, which was capable of dealing with hard foods. There was a reduction in molar size in *Homo rudolfensis* relative to *Paranthropus*, but earliest *Homo* was nevertheless comparatively megadont, illustrating that while a larger and more possibly more cognitively complex brain may have helped early *Homo* to respond to changing environmental conditions, they must still have been somewhat dependent on hard and tough vegetative resources (Wood and Strait 2004).

The evolutionary alternative to megadonty was the manufacturing and use of stone tools. The oldest chopper tools are known from Ethiopia (Hata, Bouri Formation) and from Tanzania, approximately 2.5 Ma (Kaiser et al. 1995). From Gona, east of Hadar in the Afar Triangle, primitive pebble tools are dated to 2.6 Ma (Harris 1986), and discoveries from west of Lake Turkana confirm the existence of an early tool culture around 2.5 Ma (Roche et al. 2003). Earliest cutmarks on bone fragments are reported from a 3.4-Ma-old site at Dikika in Ethiopia (McPherron et al. 2010) but have been interpreted as trampling marks by others (Domínguez-Rodrigo et al. 2010). The oldest stone tools associated with early *Homo* were found in the Hadar area of Ethiopia (Kimbel et al. 1996). At many sites the presence of more than one hominid species, occurring in the same horizon as early Oldowan pebbles, does not give clear evidence of who were the first toolmakers. However, distinct specialization of the skull and dental morphology in robust australopithecines and brain expansion in early *Homo* point to the latter as the most likely tool manufacturer (chapters "▶ Modeling the Past: Archaeology," Vol. 1 and "▶ Over view of Paleolithic Archaeology," Vol. 3).

Implements are widely used by higher primates (Boesch and Boesch 1990) (chapters "▶ Great Ape Social Systems," "▶ Cooperation, Coalition, Alliances," and "▶ Theory of Mind: A Primatological Perspective," Vol. 2). Yet during marked habitat shifts, which led to pronounced changes in food resources, it probably was the invention of stone tools which supported the origin of the genus *Homo* around 2.5 Ma. Increasing independence from the environment led to an increase in the dependence on culture.

If early *Homo* utilized stone tools to prepare food, the dentition might actually reflect these behavioral changes in food acquisition. However, the morphology of early *Homo* teeth does not seem to suggest extensive food preparation before ingestion. The incisors are large compared to those of *Australopithecus* and *H. erectus*, and the canines are large relative to the premolar crown surfaces. The premolars are narrower than in *Australopithecus* and fall within the range of *H. erectus*. Molar size overlaps the ranges for *Australopithecus* and *H. erectus*. The cheek teeth of *H. rudolfensis* are enlarged and show affinities to *Paranthropus* molars. All teeth are relatively narrow buccolingually and elongated mesiodistally, especially the mandibular molars and premolars. In *H. habilis* we see well-developed third molars, while in *H. rudolfensis*, the third molar has a smaller crown than the second molar. The occlusal surface of the cheek teeth is not as broad as in australopithecine molars and indicates differences in chewing. Tobias (1987) states that the crown's cusp relief is still present even when the teeth show advanced wear and dentine is visible. This means that the attrition of the enamel is less pronounced than in earlier hominids. Differences in tooth wear between *H. rudolfensis*, with megadont teeth and a more horizontal tooth abrasion, and *H. habilis*, with its more gracile molars and higher relief in worn teeth, are clearly visible. This indicates significant differences in diet and ecology of early *H.* species. *H. rudolfensis* and the robust australopithecines share some cranial and dental features in the morphology of the masticatory apparatus (Wood 1992), which indicates that these hominids were able to cope with hard fruits and plants. Since those features are judged as an adaptation to drier climatic conditions, they also show that *H. rudolfensis* was relatively conservative nutritionally and probably less versatile in his food choice than *H. habilis* and certainly *H. erectus* (Ungar et al. 2006).

Biogeographic Scenario

The scenario presented here is derived mainly from hypotheses about early hominid evolution in the context of environmental change and faunal biogeography. It is thus a biogeographic perspective against which we understand the relevance to studies of early *Homo* systematics in general and morphology and character transformation more specifically.

The behavioral inclination of the earliest hominids, distributed along the margins of the tropical rain forest, was to maintain a connection to, and remain near, the borders between broad riparian habitats and open woodlands during the ascendancy of more warm and humid times. Over short geological timescales, this typically involved a local, nondispersing tendency, but by approximately 4 Ma, several species of *Australopithecus* had successfully dispersed throughout the reaches of the African Rift Valley and into western Africa (Fig. 6). Over longer time frames, this included dispersal through the riparian "corridor" connecting eastern and southern Africa, permitting population dispersal into southern Africa by 3 Ma. This dispersing population maintained habitat specificities to forested environments (Rayner et al. 1993), though in more environmentally temperate climes and in relative geographical isolation at the extreme distal edge of its distribution.

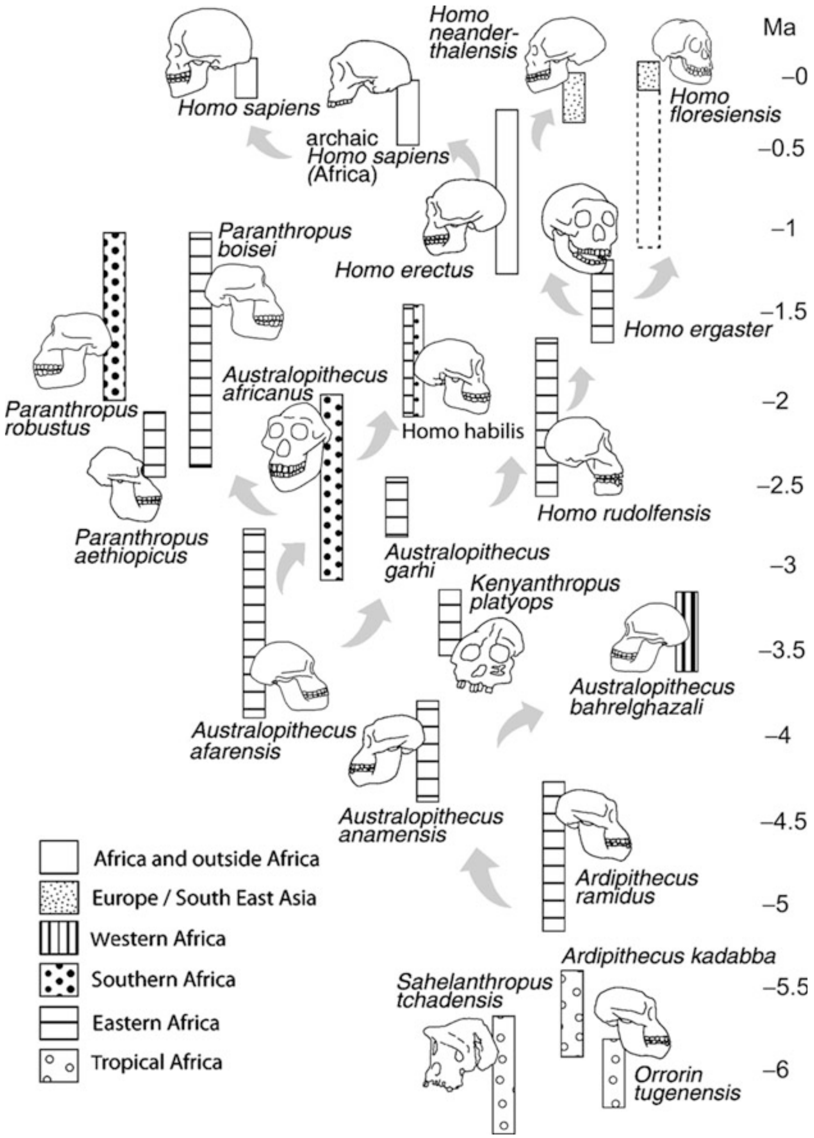


Fig. 5 Hominid chronology

The dispersion along changing latitudinal circumstances covaried with its transformation into, first, a geographic variant and, subsequently, into *A. africanus*, joining ranks with other southern African endemic faunas. Thus, *A. afarensis* was essentially an eastern African endemic form, and it follows that no typical representatives are likely to be recovered from southern African deposits older than 3.5 Ma. (Figs. 5 and 6).

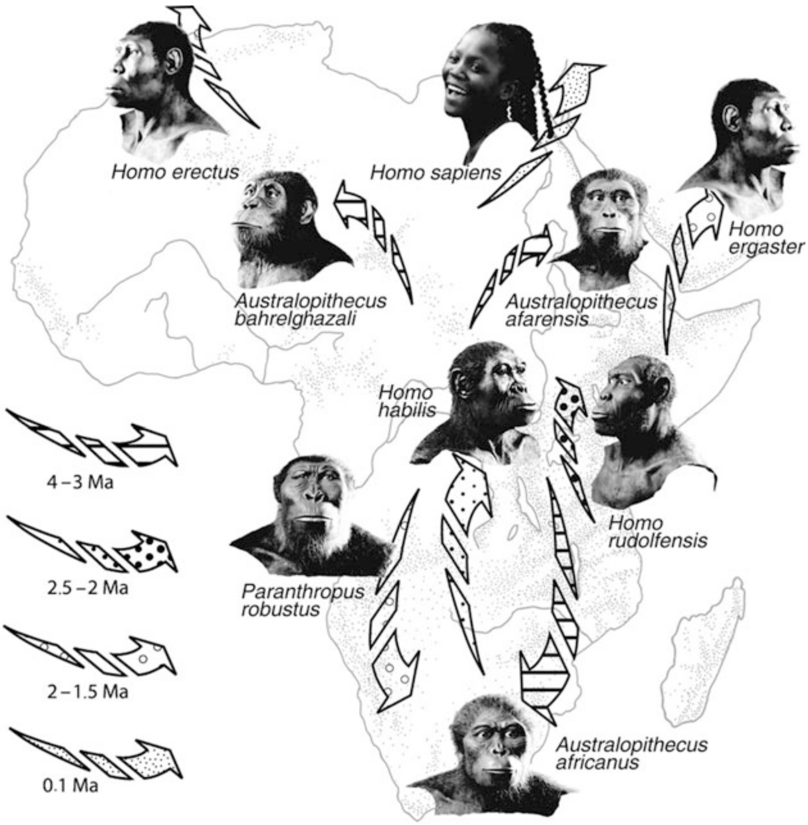


Fig. 6 Early hominid biogeography, dispersal and migration in Africa

By approximately 2.8 Ma, the initiation of cooler and drier conditions prevailed upon the African landscape, its vegetation, and its faunas, until climaxing ca. 2.5 Ma (chapters "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3 and "▶ The Paleoclimatic Record and Plio-Pleistocene Paleoenvironments," Vol. 1) (Bonnefille 1980; Vrba 1985, 1988; Prentice and Denton 1988; de Menocal 2004). During this time, *A. afarensis* in eastern Africa and *A. africanus* in southern Africa were each subject to unique paleobiogeographic consequences of this global aridification, reflected in the "Habitat Theory" of Vrba (chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3) (1992).

For *A. afarensis*, then, the changing climate meant vicariance of its habitat and its distribution into more distant ecotonal riparian and closed lake margin environs. During the interim between ca. 2.8 and 2.5 Ma, these changing conditions engendered more extensive open habitats, comprising more resistant arid-tolerant vegetation around the remaining relatively lush but narrowed "ribbons" of tree-lined riverine forest. The selective pressures of this habitat change resulted in the increased survival of more megadont varieties capable of feeding on harder fruit and open woodland-open savanna food items. This was so for early hominid as well as numerous eastern and southern African large terrestrial vertebrate lineages ca. 2.5 Ma (Turner and Wood 1993). These pressures were likewise sufficient to result in the phyletic splitting of *A. afarensis* into *Paranthropus* and *Homo* lineages by ca. 2.5 Ma (Vrba 1988) (Figs. 5 and 6).

Ensuing cooler and drier conditions favored a savanna vegetation composed of plant species better able to retain their moisture under such conditions. Selection favored more facially robust and large molar-toothed mammals, including early hominids, capable of efficiently processing harder, more durable vegetation of the savanna. Our evidence suggests that the tropical equatorial animals, including the hominids, of eastern Africa stay in the tropical African ecological domain, while during the drying and cooling of global climates ca. 2.5 Ma, the southern and more temperate African faunas follow their northward-drifting vegetation zones. Thus, *Homo* and *Paranthropus* may have emerged in tropical Africa as a result of the ca. 2.5-Ma climatic cooling event and remained endemic to tropical latitudes during this time (Bromage et al. 1995). The eastern African tropical faunas, having habitable alternatives, remained within their biogeographic domains rather than braving the relative deterioration and paucity of habitats south of the African Rift Valley.

The faunas of southern Africa were subject to a different set of environmental stimuli during the ca. 2.5-Ma cooling event. Waning of the forests and woodlands and expansion of more open arid grasslands not only invigorated evolutionary adaptations to savanna life in tropical eastern Africa but also resulted in the distribution drift northward of faunas that tracked the equatorial shift of grassland and woodland biomes into eastern Africa from the south, ca. 2.5 Ma (Bromage et al. 1995). The temperate zone ca. 2.5 Ma experienced more seasonal extremes, and many organisms unwittingly maintained their inherited preference for moderate seasonal climes and temperate vegetation by moving northward with the shrinking of this biome toward the equator, effectively transgressing the Zambezi Ecozone. Among these migrants was *A. africanus* which, having been adapted to a modest temperate ecology, now found its suitable habitats shifted to the north toward the East African Rift Valley. While dispersing toward the eastern African tropical domain, selection for increased behavioral flexibility was related to the habitat diversity of the tropics and the presence of other non-vegetative food resources available in their new region. This emerging taxon, *H. habilis*, rapidly established itself as a categorical omnivore and found that it could buffer itself more resolutely from environmental changes (Ungar et al. 2006). This enabled it to cross habitat boundaries more easily and also to advantage itself of more resources with its material culture.

By approximately 2 Ma, Africa was rebounding from its relatively cool and dry climate to return to slightly more warm and humid conditions (Bromage et al. 1995). A phase of biome expansion ensued, which facilitated dispersions away from the equator, ending nearly 1 Myr of relative endemism dominated by tropical equatorial speciations. *P. boisei* dispersed southward, along reestablished ecotonal habitats, into southern Africa, became a geographic variant under more temperate conditions, and evolved into *Paranthropus robustus* (Fig. 5). *Homo habilis* expanded southward into the southern African temperate domain, but it maintained a very much broader niche and increased its distributional area as a single species. *Homo rudolfensis* remained endemic to the eastern African tropical domain due partly to its preference for more open habitats around the rain shadows of the African Rift Valley and partly, perhaps, to some small measure of competitive exclusion from geographic realms occupied by *H. habilis*.

Whereas our model suggests the origin of early *Homo* in tropical (eastern) Africa, recent fossil discoveries from Malapa Cave South Africa (Berger et al. 2010), described as *Australopithecus sediba*, have been interpreted as potential evidence for a Southern African origin of *Homo*. The hip structure of this species seems more closely related to *Homo erectus* than to *Homo rudolfensis* or *Homo habilis*. However, with an age of less than 2 Ma, it seems more likely that these late australopiths were convergently adapted with rather than ancestral to the earliest *Homo*.

Conclusions

The origin of the genus *Homo* is highly debated. Earliest fossil evidence dates to around 2.5 Ma and is in temporal co-existence with the appearance of *Paranthropus* in eastern Africa. The beginning of the *Homo* lineage, represented by *H. rudolfensis*, was an endorsement of its recency of common ancestry with *A. afarensis*, a distinction it shared with *Paranthropus*. However, while *Paranthropus* was principally adapted by means of a robust masticatory system to abrasive diet, early *Homo* exhibited an increased behavioral and dietary flexibility as its adaptation included a larger and more provoking, inquiring, and capable brain, which led to a large diversification represented by later *Homo* species, such as *H. habilis/ergaster/erectus*. This included a shift to proportionately less abrasive foodstuffs and more omnivorous habits. Increasing cultural abilities and the beginnings of a stone tool culture ameliorated the effects of changing habitats and food resources to the degree that it enabled early *Homo* to take advantage of diverse resources more efficiently than was ever possible before.

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Homo ergaster and Its Contemporaries

Ian Tattersall

Contents

Abstract

On the basis of their strong morphological differences from the Javan type materials, many authorities now consider the diverse East African fossils initially classified as "African *Homo erectus*" to be more properly allocable to the species *H. ergaster*. However, while this separation at the species level of the African and Indonesian hominids is certainly justified, the species *H. ergaster* as thus constituted still embraces a significant morphological variety. Indeed, although this grouping of African fossils seems to form a fairly coherent clade, it also appears quite diverse. The East Turkana type mandible of *H. ergaster* is matched by other specimens from Kenya and Tanzania, but not by the mandible of the iconic WT 15000 skeleton, and in its turn this specimen fails to match either in its cranial construction or its upper dentition most of the other comparable specimens usually referred to *H. ergaster*. Clearly there is a need for a systematic reappraisal of the entire "African *Homo erectus*" = *Homo ergaster* group, and equally clearly the hominid evolutionary story throughout the Old

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I. Tattersall (✉)
Division of Anthropology, American Museum of Natural History, New York, NY, USA
e-mail: iant@amnh.org

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World in the Early–Middle Pleistocene was more complex than is implied by the extension of the species *H. erectus* to cover the entire miscellaneous assemblage of hominid fossils from this time period.

Introduction

There is probably no area of paleoanthropology in which disagreement is more profound than in the systematics and taxonomy of the genus *Homo* in the Early to Middle Pleistocene. This discord has a long and, dare one say it, illustrious pedigree, dating right back to the initial discovery and description of the Javan species *Pithecanthropus* (=*Homo*) *erectus* by Eugène Dubois in the early 1890s. At that time the only extinct hominid known was the European *H. neanderthalensis*, a form that, though peculiar in morphology, possessed a brain of modern human size. The new and more ancient hominid announced by Dubois as an intermediate between modern humans and apes (a status reflected in his initial choice of name, which translates as "upright ape-man") was thus the first known human fossil relative to display a brain cavity that was significantly larger than those of modern-day great apes while lying below the range of *H. sapiens*. Dubois's discovery unleashed an immediate furor. The key to Dubois's interpretation of this specimen as a human relative (though he stopped short of placing his find in the human family Hominidae) was the association of the type Trinil skullcap with a femur whose morphology was without doubt that of an upright biped in the modern fashion. This association was immediately attacked (and has continued to be periodically questioned), initially by those who preferred to see the cranium as that of a specialized ape, maybe related to the gibbons. At the same time, many of those who accepted the association between the cranium and femur wrote off the former as deriving from an aberrant modern human (see discussion in Tattersall 1995, 2008).

Still, some paleoanthropologists (Cunningham 1895) did seize immediately upon the Trinil specimen as an evolutionary intermediate between great apes and humans, and were willing to view the Javan hominid as an early member of a lineage that had given rise to *H. sapiens* via the Neanderthals. This interpretation rapidly gained ground (Theunissen 1988), and by early in the twentieth century, not least through the efforts of Schwalbe (1899) – and despite those of Boule (1911–1913) – the place of *H. erectus* as the "hominid in the middle" had effectively been secured. Given the tiny size of the hominid fossil record at that time, and that the apparent rudiments of a transformation series in brain size were present in what was known, this interpretation was hardly surprising: indeed, it was a good story that was hardly contradicted by the few facts then available. And, in the decades before the Second World War, two additional developments conspired to keep *H. erectus* at the front and center in scenarios of human evolution.

The first of these was the discovery of the huge trove of *Sinanthropus pekinensis* fossils at Zhoukoudian near Beijing during the late 1920s and the 1930s, and of the similarly impressive series of *H. soloensis* crania at Ngandong in Java in

1931–1932. The hominids from both sites were reckoned to be very close to Javan *H. erectus*, if not exactly the same thing; and at a time when most hominid fossil sites produced a specimen here and there, both discoveries were overwhelming by virtue of the sheer volume of material produced. At the same time geneticists, systematists, and paleontologists in the USA and Europe were busily constructing the outlines of what came to be known as the Evolutionary Synthesis, which saw the gradual modification of continuous lineages as the central feature of the evolutionary process (see discussion in Tattersall 1995). And at mid-century, the ornithologist Ernst Mayr (1950), one of the principal architects of the Synthesis, bluntly told the paleoanthropological profession that *S. pekinensis*, *H. soloensis*, and other Middle Pleistocene hominids all belonged to *H. erectus*, the species that occupied the middle part of a direct and gradually transforming lineage running from *H. transvaalensis* (the australopiths) at the beginning to *H. sapiens* (which embraced the Neanderthals) at the summit.

Mayr's short article was perhaps the most influential contribution ever in paleoanthropology, and effectively set its agenda for the next half-century. The rapidly increasing size of the human fossil record eventually forced even Mayr to relent, and to admit a little more complexity into the picture; but for decades, paleoanthropologists labored steadfastly under the notion that the evolutionary history of our kind had largely involved the gradual modification through time of a central lineage that eventually culminated in *H. sapiens*. Of course, it was admitted that at any one point in time such a lineage, widely distributed across the Old World, would have harbored a variety of local variants (see Baab, chapter "▶ Defining *Homo erectus*," Vol. 3); but throughout the second half of the twentieth century, the emphasis was principally on within-species variation, rather than on the question of whether a signal of systematic (species) diversity might be detectable in the variety of morphologies that emerged as the hominid fossil record steadily enlarged. Against this background, the category *H. erectus* became a catchall for a huge and unwieldy assortment of fossils of substantially differing morphologies.

Such hominids came from widely scattered localities. First, the probably 1.0- to 0.7-million-year (myr)-old Trinil specimens from Java were joined by a steady stream of discoveries in the nearby Sangiran Dome, not far away, that probably date in the 1.5- to 1.0-myr range, most of them closer to its younger end. Then the sample was augmented by the Chinese Peking Man fossils, now thought to be probably between about 500 and 300,000 years (kyr) old, followed by the Ngandong specimens (which may be as young as 50–30 kyr old), and ultimately by other Javanese fossils from localities such as Sambungmacan and Ngawi, both uncertainly dated but unlikely to be more than 200 kyr old, and most probably younger. In China, later finds attributed to *H. erectus* came from sites including Lantian (Gongwangling and Chenjiawo, both perhaps around 1.0 myr), Hexian (maybe 400 kyr), Nanjing (ca. 350 kyr), and even Longgupo, a site that may possibly be as much as 1.8 myr old. Some European specimens in the 400–300 kyr range, such as those from Vértesszöllös (Hungary), Arago (France), and Bilzingsleben (Germany), have been referred by some authors to *H. erectus*, as has the 900- to 800-kyr-old calvaria from Ceprano in Italy. Further east, in the Caucasus, the 1.8-myr-old Georgian site of Dmanisi has yielded fossils that have also been attributed to *H. erectus*. In Africa practically anything from the earlier Middle Pleistocene, and soon many older specimens as well, found themselves identified as *H. erectus*, so that the species came to include such motley fossils as the 1.4-myr-old Olduvai Hominid (OH) 9 calvaria from Tanzania; the 700-kyr-old mandibles from Tighenif (Ternifine) in Algeria; the 400-kyr-old Salé partial braincase from Morocco; the 1.6-myr-old WT 15000 "Turkana Boy" skeleton from Nariokotome on the western side of Lake Turkana in Kenya, and several crania and mandibles in the 1.9–1.5-myr range from Koobi Fora and Ileret on the eastern side of the same lake; also from Kenya, the fragmentary Olorgesailie hominid at 1.0–0.9 myr; the 1-myr-old Daka calvaria from Ethiopia; a cranium of apparently similar age from Buia in Eritrea; and even, from South Africa, the perhaps 1.6-myr-old Swartkrans Member 1 SK 847 partial cranium.

Not only do these fossils cover an enormous span of time (ca. 1.8–0.03 myr), but they also embrace a huge range of morphologies, and taken together they hardly suggest a neat chronological series of the kind the Synthesis had predicted. Clearly, there is a systematic signal of some kind in the assemblage of hominid fossils that have at one time or another been allocated to *Homo erectus*: a signal of diversity at the species as well as the morphological level. But it was not until the beginning of the final quarter of the twentieth century that this possibility began to be seriously investigated.

Enter *Homo ergaster*

The existence of *H. erectus* as a convenient catchall for a remarkable variety of hominids certainly facilitated the telling of a relatively simple and straightforward human evolutionary story that could be told in terms of consistent long-term selection pressures for such things as more perfect thermoregulation, more efficient digestion, and above all greater intelligence. However, this story of the gradual honing over time of an ever more effective human machine was contradicted by the growing post-Synthesis realization that the evolutionary process consists of a great deal more than simple natural selection (Tattersall 1995, 1998). It also sat rather uneasily with the fact that the Pleistocene was increasingly being seen as a period of extraordinary short-term climatic oscillations as well as of longer-term fluctuations (see Van Couvering, chapter "▶ Quaternary Geology and Paleoenvironments," Vol. 1). And, most significantly of all, it was not the story that the growing assemblage of *Homo* fossils seemed to be telling.

The first shot across the bows of the all-encompassing notion of *H. erectus* came from work on fossils found at the classic African localities on the eastern shores of Lake Turkana. During the 1970s, several fossils, notably the partial crania KNM-ER 3733 and KNM-ER 3883, were discovered at Koobi Fora that their

Fig. 1 Lateral view of the KNM-ER 992 holotype mandible of *H. ergaster*. Scan of cast by Ken Mowbray

describers (Leakey and Walker 1976; Walker and Leakey 1978) ascribed to the species *H. erectus*. With cranial volumes of 848 and 804 ml respectively (these and most of the other endocranial volumes cited here come from Holloway et al. 2004), these 1.8- and 1.6-myr-old individuals had possessed brains almost as large as that of Dubois's much younger (1.0–0.7 myr) Trinil type specimen of *H. erectus*, at about 950 ml. Another significant specimen was a well-preserved mandible, KNM-ER 992 (Fig. 1), about 1.5 myr old, which was recovered at Ileret and described simply as *Homo* of indeterminate species (Leakey 1972). Soon thereafter, Groves and Mazák (1975) jumped into the fray and made ER 992 the type specimen of a new species, *H. ergaster*. Although this innovation was disdainfully dismissed by the Koobi Fora team, and some other influential workers (Rightmire 1990) also continued to prefer the more comprehensive concept of *H. erectus*, this move finally opened the door to a reappraisal of the tradition of automatically assigning to *H. erectus* any and all African fossils with measured or assumed brain sizes in the general range of those noted above. In short, it became possible to entertain the notion that *H. erectus* is a terminal eastern Asian hominid species, and that hominid evolution throughout the Early and Middle Pleistocene continued in the pattern already established, with a vigorous exploration of the many different ways in which it was possible to be a hominid in the shifting and highly varied habitats of the Ice Age Old World. The next section, on "Cranial Morphologies in *Homo* of the Early to Middle Pleistocene," will examine the morphological evidence for diversity within the immediate group to which both *H. ergaster* and *H. erectus* belong.

Cranial Morphologies in *Homo* of the Early to Middle Pleistocene

General Considerations

Nobody doubts that the *H. erectus*/*H. ergaster* group represents a relatively cohesive subset of the family Hominidae. The question, clearly, is whether in this group of fossils we are looking at a radiation of species or at a single hugely variable species that may or may not have evolved directionally over the entire expanse of time (about 1.9–1.8 to 0.03 myr) and space (virtually the entire habitable Old World) it occupied. The distinction here is an important one, for species (even if not greatly differentiated morphologically from their closest relatives) are historically individuated entities which can compete with one another for ecological space and become extinct, whereas within species even demes that are significantly differentiated morphologically remain ephemeral entities that can disappear simply by absorption into ongoing conspecific populations. The twin processes of speciation and genetic/morphological differentiation are not linked, so that speciation may take place in the absence of significant morphological divergence, while the latter can occur without speciation intervening. This, of course, often makes unequivocal species recognition difficult in fossil assemblages (Tattersall 1986). However, it seems generally to be the case among living primates that, where substantial osteological differences are present among populations, those populations tend to act in nature as distinct species (i.e., as effectively independent reproductive entities). If we apply this criterion very conservatively to species recognition in the fossil record, demanding that the fossil species we recognize consistently bear distinctive osteological differences from related forms, we will probably underestimate the number of species in that record. However, we will not distort its overall pattern (Tattersall 1986, 1992). It is important to bear in mind that not all "morphs" (distinctive morphological entities) that we recognize in the fossil record will necessarily correspond to species in the reproductive sense; but it is equally evident that, given the nature of the fossil record, morphology must be the starting point in our analyses of it. After all, neither geological age nor geographical provenance, the other two attributes of any fossil, is *necessarily* linked to species identity, while its morphology is the only feature that makes a fossil species recognizable at all. It is in this spirit that the remainder of this survey is offered, with the proviso that we will clearly not learn much that is useful about the pattern of events in hominid evolution during the Pleistocene if we do nothing more than replace the term "African *Homo erectus*" with the equally sweeping *H. ergaster*.

Eastern Asia

Given the established conventions of nomenclature and systematics, when we begin to consider the mass of material that has at one time or another been allocated to *H. erectus*/*H. ergaster* we must necessarily begin with Dubois's holotype material

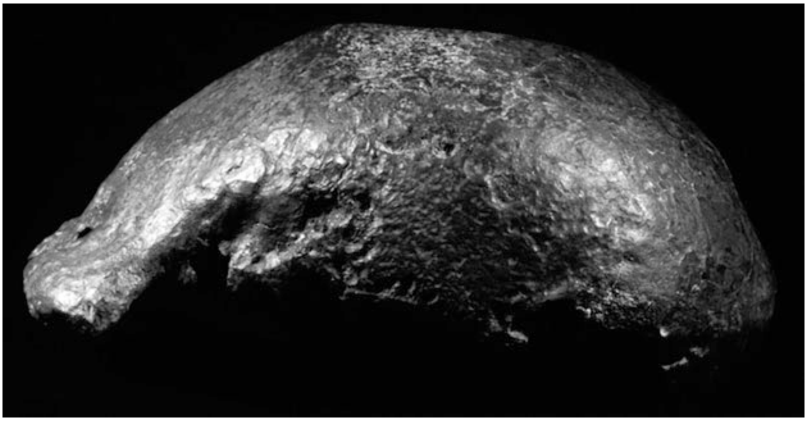

Fig. 2 Lateral view of the Trinil holotype calotte of *H. erectus* (Photo courtesy of © Jeffrey H. Schwartz)

(Fig. 2) from Trinil in Java (Schwartz and Tattersall 2003, 2005). It is the morphology of the Trinil skullcap that defines the species *H. erectus*, and the allocation of other fossils to this named entity must be done on the basis of their morphological similarities to it. The problem lies, of course, in deciding just how close those similarities should be, and it has to be admitted that there is no quantifiable answer to this question.

The Trinil 2 holotype is highly derived among hominids in a number of characteristics, especially of the brow region and the rear of the skull (Schwartz and Tattersall 2000, 2005). It is a smallish, long, thin-boned calotte with a narrow, shelflike, and laterally flaring postorbital region that flows onto the long, gently sloping, and flattish frontal plane with an almost imperceptible midline keel defined by shallow depressions bilaterally. The lateral walls of the low braincase are short and are markedly tilted inwardly above faint, low-set temporal lines; and the rather acute nuchal angle is distended posteriorly into a well-defined horizontal torus. Although the hominid sample from the adjacent Sangiran region is quite variable, especially in robusticity, the basic Trinil braincase morphology is repeated in most of the crania, the major exception being the quite complete if somewhat distorted cranium Sangiran 17 (Fig. 3). The Sangiran sample of upper and lower dentitions is also heterogeneous, suggesting that a second hominid morph may be present in addition to the Trinil one.

The two (now three) crania known from the Sambungmacan region, to the northeast of Sangiran, are substantially younger than the Trinil/Sangiran assemblage and share a contrasting brow structure in which the quite horizontal supraorbital tori thicken laterally and appear to be continuous across glabella. The braincase itself has the appearance of being rather better inflated than typical of the Trinil form (the two published brain volumes are 1,035 and 917 ml), and the coronal profile is tent-shaped rather than having a squat and rounded outline. The nuchal plane undercuts the occiput to produce a horizontal torus that is well defined

Fig. 3 Lateral views of crania from Africa and Eurasia in the "*Homo erectus*/*Homo ergaster*" group. *Left column*, *top* to *bottom*: Sangiran S17; Koobi Fora KNM-ER 3733; Koobi Fora KNM-ER 3732; West Turkana KNM-WT 15000; Dmanisi D 2282. *Right column*, *top* to *bottom*: Zhoukoudian cranial reconstruction (Sawyer and Tattersall version); Koobi Fora KNM-ER 3883; Olduvai OH 9; Koobi Fora KNM-ER 1813 (scale = 1 cm) (From Schwartz and Tattersall (2005). Photo courtesy of © Jeffrey H. Schwartz; Turkana fossil images courtesy of National Museums of Kenya)

below, but has much poorer definition above. Together these specimens, along with another calvaria from Ngawi (870 ml), produce a morph that generally resembles the Trinil type but is readily distinguishable from it. The Ngandong crania are similarly distinctive. Larger and more robust than the others, with endocranial volumes that range from 1,015 to 1,250 ml, they differ from the Trinil form in the ways in which the Sambungmacan ones do. However, in addition they present yet more capacious braincases that have more or less vertical side walls with quite aggressively raised temporal lines; and they show a greater rearward projection than the Sambungmacan forms do of the occipital torus, a feature with a well-defined superior border. Nonetheless, this entire group is united, in particular, by a set of derived supraorbital and nuchal morphologies, and it presents itself as a relatively cohesive whole. Clearly, these Javan forms are part of the same eastern Asian hominid clade and, if it is not divided up (basically, at this point, a matter of taste), it is this assemblage that must provide the core identity of the species *H. erectus*.

The hominid fossils from Locality 1 of Zhoukoudian, in China (Fig. 3), have generally been considered classic exemplars of *H. erectus*. But it is still worthwhile noting that as a group they do differ fairly markedly from the Trinil type material, though mostly in ways that recall the Sambungmacan/Ngandong series. The crania from this site (with brain volumes ranging from 850 to 1,140 ml) are most distinctive in their supraorbital morphology, with a low-set glabella, supraorbital tori having a strong vertical component, and a continuous posttoral sulcus. In addition, there are marked dental differences between the Zhoukoudian and Sangiran samples (Schwartz and Tattersall 2005). Chinese specimens closely resembling the Peking Man materials include the Nanjing crania (Lü and the Tangshan Archaeological Team 1996). Other materials sometimes associated with them, such as those from Lantian, Hexian, Yunxian, and Longgupo, show a variety of differences both from Zhoukoudian and among themselves. These differences are discussed by Schwartz and Tattersall (2005) and Tattersall and Schwartz (2009).

Africa

As already noted, at one time or another many African fossils in the 1- to 2-myr time range have been referred to the species *H. erectus*. Among them, the classic exemplars are fossils from the Turkana Basin of northern Kenya, notable among these being the cranium KNM-ER 3733 and the calvaria ER 3883 from sediments at Koobi Fora to the east of Lake Turkana, and the fairly complete skeleton KNM-WT 15000 from deposits to its west at Nariokotome. The mandible KNM-ER 992, initially allocated simply to *Homo* sp., comes from Ileret, to the north of Koobi Fora. All the specimens concerned date within the 1.9- to 1.5-myr range. The widely used term "African *Homo erectus*" was a convenient designation for these fossils and a host of others, but it disguises the fact that a substantial variety of morphologies is involved.

Fig. 4 Occlusal views of mandibles. *Top left*: left side of Koobi Fora KNM-ER 992. *Top right*: Koobi Fora KNM-ER 3734. *Middle left*: Olduvai OH 22; *Middle right*: left side of West Turkana KNM-WT 15000. *Bottom*: left side of Dmanisi D 211 (scale = 1 cm) (From Schwartz and Tattersall (2005). Photo courtesy of © Jeffrey H. Schwartz; Turkana fossil images courtesy of National Museums of Kenya)

This reality was first acknowledged in 1975 by Groves and Mazák who, as noted, made the ER 992 mandible (Figs. 1 and 4), the holotype of the new species *H. ergaster* ("work man"). Subsequently, many authors have begun to use the new name in place of "African *Homo erectus*," to the extent that it is now *H. ergaster* that is the standard-issue *Homo* of the 2- to 1-myr period. Still, all this change has achieved is to remove the assortment of Asian morphologies from the African equation, and it does nothing to address the morphological variety found within the continent in this period. In coming to grips with this, the best place to start is with the iconic example, the KNM-ER 3733 cranium (Fig. 3), which has an endocranial capacity of 848 ml. In this individual, the supraorbitals arc separately over each orbit and project forward as well as upward. There is thus a distinct posttoral sulcus in front of the quite steep frontal rise, which rapidly peaks before the profile descends more gradually rearward. Seen from behind, the braincase is rather tall compared to its breadth, and its side walls are curving. The raised temporal lines start quite far medially. It is unsurprising that these characteristics distinguish this specimen sharply from any Asian *Homo*; more remarkable are its differences from the ER 3883 cranium (Fig. 3), which has an endocranial volume of 804 ml. This individual has very thickened supraorbital margins that protrude outward but slightly down, overhanging nasion and the (mostly missing) face beneath. Further, in this specimen the frontal slopes strongly up and back, reaching its maximum height rather far back. Unlike in ER 3733, the mastoid is large and protruding, and in what is preserved of the face the zygoma flares outward from top to bottom. That this morphology is no freak is shown by its close repetition in preserved features of the ER 3732 partial cranium (Fig. 3).

Interestingly, all the specimens just mentioned are distinctly different from the skull of the KNM-WT 15000 skeleton (Fig. 3), exhaustively described in the monograph edited by Alan Walker and Richard Leakey (1993). This 1.6-myr-old skeleton is remarkable both for its degree of completeness and for being the earliest good evidence we have in the human fossil record of the arrival of essentially modern stature and postcranial proportions. Frustratingly, we cannot yet be certain that this was the case for the possessors of the ER 3733 and ER 3883 crania. The adolescent WT 15000 individual died at about 8 years of age, but was at a stage of development approximating that of a modern 12-year-old. This presumed male stood about 160 cm tall, but had he survived to adulthood, it is estimated that he would have topped 180 cm. He was long limbed and slender, with efficient heat-shedding proportions that would have served him well in the heat of the open tropical savanna. In contrast to the relatively long crania just described, the braincase of WT 15000, with a capacity of about 900 ml, was quite short and had a well-rounded profile. To the extent that it is possible to judge, the badly damaged supraorbital surfaces amounted to little more than substantial thickenings of the superior orbital margins, lacking either the aggressive projection seen in ER 3733 or the vertical thickening noted in ER 3883. The structure of the face contrasts with that seen in both ER 3733 and ER 3883; it is longer and narrower, with much more alveolar prognathism, a higher and narrower nasal aperture, and preserved portions of the nasal bones that suggest a flatter profile of the upper face. It is often claimed that these differences from the East Turkana specimens are due to the subadult status of WT 15000, but this appears rather dubious since differences of this kind would, if anything, probably have become more marked with age.

Cranial differences are backed up by dental comparisons to the extent that these are possible. ER 3883 has no associated teeth, and ER 3733 has only one, an M^2. But this tooth, though unfortunately quite heavily worn, is nonetheless distinctly different from its counterpart in WT 15000. The M^2 of ER 3733 has smooth enamel and well-defined trigon cusps, with the paracone much larger than the metacone. The hypocone is distally placed, the cristae are sharp, and both basins are well excavated. In WT 15000, in contrast, the M^2s are high-crowned, with fairly flat but wrinkled occlusal surfaces. The cusps of the trigon are subequal in size, and the basins are quite shallow. In both ER 3733 and WT 15000, the M^2s contrast with their homologues in the best-preserved upper dentition from Java, the Sangiran

4 palate, in which there are low cusps, a massive hypocone, and a very large postprotocrista that is not a feature of either African specimen.

The ER 992 type specimen of *H. ergaster* is a lower jaw, so comparisons to ER 3733 and ER 3883 are not possible. However, uniquely, the WT 15000 skull has a definitively associated lower jaw (Fig. 4), allowing direct comparison to ER 992. When this comparison is made, clear differences become apparent. In ER 992 (Fig. 4), the lower canines are quite high and are compressed buccolingually. In the anterior lower premolar, there are distinct anterior and posterior foveae, and the protoconid is the clearly dominant cusp. In the posterior premolar the protoconid and metaconid are subequal, and the basins are shallow. The elongated lower molars bear rounded and protruding hypoconulids, their basins are shallow, and their enamel is wrinkled. In contrast, the lower canines of WT 15000 are short crowned, with distinct mesial and distal foveae that bound a strong lingual pillar that swells out the tooth at its base. Both premolars have deep mesial and distal basins. The first molar is distended mesially, and both erupted molars have large and lingually placed hypoconulids and narrow but deep talonid basins that are surrounded by well-defined but rather bulbous cusps. Here, again, we have two distinctly different lower dental morphologies, both of which also differ from their homologues known from Sangiran. Morphologically, at least, the lower dentitions of ER 992 and WT 15000 are not “the same thing,” and both are at variance with Javan *H. erectus* (Schwartz and Tattersall 2000, 2005).

Interestingly, the 1.5-myr-old ER 992 from Ileret makes a fairly good match for the mandible OH 22 (Fig. 4) from Olduvai Gorge in Tanzania, as well as for its rather older (1.9 myr) neighbor ER 3734 (Fig. 4) from Koobi Fora. As for WT 15000, its lower teeth compare quite closely with those of OH 13, one of the paratypes of *H. habilis* from Bed II of Olduvai Gorge, and of similar age. Both show mesially tapering premolars, with small metaconids lying opposite the protoconids, and smaller foveae in front of these cusps than behind. The degree of wear on the molars is very different, but both show an oblique groove that runs between the hypoconulid and hypoconid to the base of the metaconid; and in both the hypoconid lies buccally and the M_1s taper slightly distally, while the M_2s are more broadly rounded at the rear. In the cranium and upper dentition, WT 15000 shows substantial similarities with the East Turkana cranium ER 1813 (Fig. 3). Although the latter boasts a substantially smaller intracranial volume of 510 ml, both specimens share a short, high cranial vault (rather like that of OH 13) with rounded brows that arc over each orbit and a frontal that rises behind a very short posttoral plane. In both the nasal apertures are tall, are relatively narrow, and taper strongly upward, while the nasoalveolar clivuses are long and slope forward.

Even more telling are upper dental similarities among WT 15000, ER 1813, and OH 13. All have a high-crowned but flat-surfaced M^1, with the mesiodistally long hypocone as high as the protocone, and separated from it by a lingual notch. In all, the M^2s are basically similar to the M^1s, but show reduction of the metacone and a smaller notch between the hypocone and protocone. In all, M^1 and M^2 both have thick postcingula. In WT 15000 and ER 1813, the P^2s are very similar in having a bulbous and centrally placed paracone and a continuous crista running mesially from the paracone and swinging right around the side of the tooth. Further, although it has a very worn dentition, the recently described palate OH 62 seems to present an upper dental morphology similar to those of the three specimens just described. In sum, the evidence seems to be quite compelling for the existence of an upper dental morph, most spectacularly represented by the fairly complete individual WT 15000, that is found almost a thousand kilometers away at Olduvai as well as around Lake Turkana at Koobi Fora and Nariokotome. The available name for this morph, should anyone wish to designate it a species, is *H. microcranous* (Ferguson 1995).

Other "African *Homo erectus*" specimens include the 1.4-myr-old OH 9 calvaria (Fig. 3: 967 ml) from Olduvai Gorge, but it does not compare any better to the material from eastern Asia than it does to the Turkana fossils; and though it has been compared to the purportedly *H. erectus* Daka cranium from Ethiopia (~1.0 myr, 995 ml; Asfaw et al. 2002), resemblances between the two, other than in endocranial volume and its correlates, are not particularly striking (Schwartz and Tattersall 2005). In sum, there is considerable morphological diversity among African *Homo* of the 2.0- to 1.0-myr period; and this diversity does seem to be organized into a number of distinctive morphs. Some of these are represented by individual fossils such as OH 9 that are clear outliers in terms of other known material; others seem to be represented by multiple individuals and even at multiple sites. Definitive systematic organization of this variety will clearly have to await a more comprehensive fossil record, but it is already evident that we are not looking here at a chronological transformation series, even one that is represented by high diversity at all time points. Somewhere in all of this there is a systematic signal, and it is evident that the blanket appellation *H. ergaster*, while a useful device for distinguishing the African hominid radiation of this period from the Asian one, is an inadequate expedient for describing diversity in the African record.

Some paleoanthropologists are beginning implicitly to recognize this, but apparently without wishing to abandon old paradigms. Thus Spoor et al. (2007) reported new fossils from East Turkana that they concluded were evidence for two contemporaneous lineages of *Homo* in the Turkana Basin at around 1.5 million years ago. One of these was the calvaria KNM-ER 42700. Spoor and colleagues cited a handful of trivial features that they claimed allied this specimen with *Homo erectus*; but in reality it bears none of the classic hallmarks of that species such as the long, low, posteriorly sharply angled lateral profile, the shelflike and protruding supraorbital surfaces, and the ovoid posterior profile. Indeed, in these diagnostic features the Turkana specimen is the very antithesis of the Javan type specimen. In contrast, the partial maxilla KNM-ER 42703, though hardly comparable to the calvaria, was considered to represent another lineage and was allocated to the exceedingly poorly defined species *Homo habilis*. Whether or not that species assignment is appropriate, or even means anything at all, the allocation of ER 42700 to *Homo erectus* is extremely telling. For while Spoor and colleagues evidently accept diversity among 1.5-myr-old hominids at Turkana, the assignment of the calvaria to *Homo erectus* only makes any sense at all in the context of the notion that *Homo erectus* is the middle "grade" of a single comprehensive, worldwide, variable, and gradually evolving *Homo* lineage.

Europe

It is now fairly widely accepted that most of the western European forms that have at one time or another been described as *H. erectus* (see above) are better allocated to *H. heidelbergensis*, a move that takes these fossils out of the scope of the current discussion. And while some still view the Italian Ceprano calvaria (ca. 800–900 kyr; 1,165 ml), recently designated the holotype of *H. cepranensis* by Mallegni et al. (2003), as a representative of *H. erectus*, nobody has claimed that it represents *H. ergaster*. Indeed, Mounier et al. (2011) have suggested that it is a primitive *Homo heidelbergensis*.

To the east, however, in the Caucasus at the Georgian site of Dmanisi (1.8 myr), there exists a very important and early hominid fossil assemblage with claimed African affinities (Figs. 3, 4, 5, 6, and 7). The first find, the mandible D 211 (Fig. 4) discovered in 1991, was assigned by its describers to "archaic African *Homo erectus*" (Gabunia and Vekua 1995). It was more generally attributed to

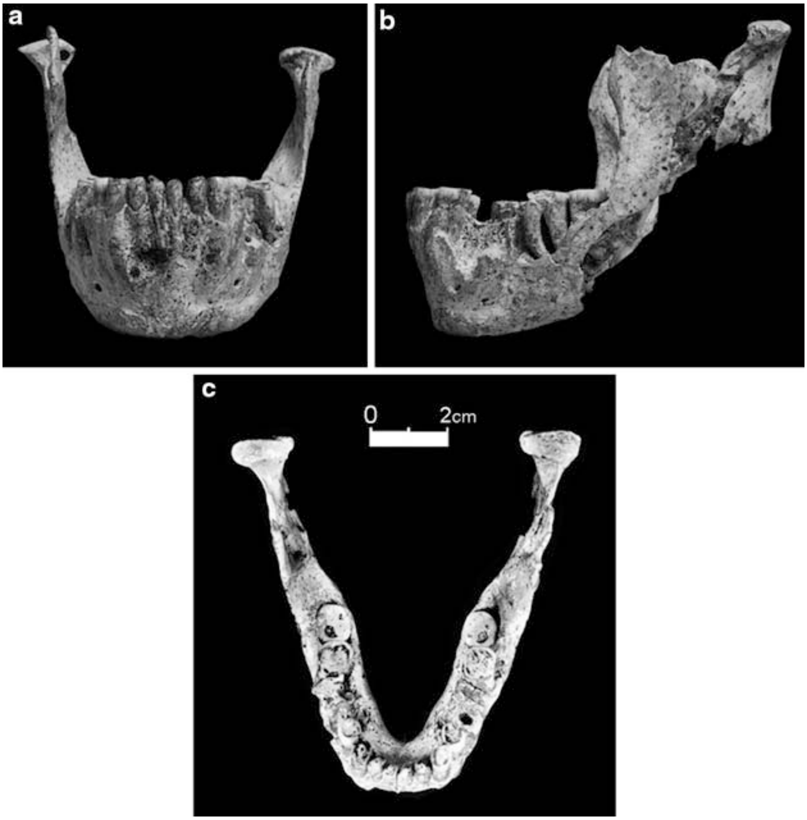

Fig. 5 The D 2600 mandible from Dmanisi. (**a**) Front view, (**b**) left lateral, and (**c**) occlusal (Photos courtesy of David Lordkipanidze)

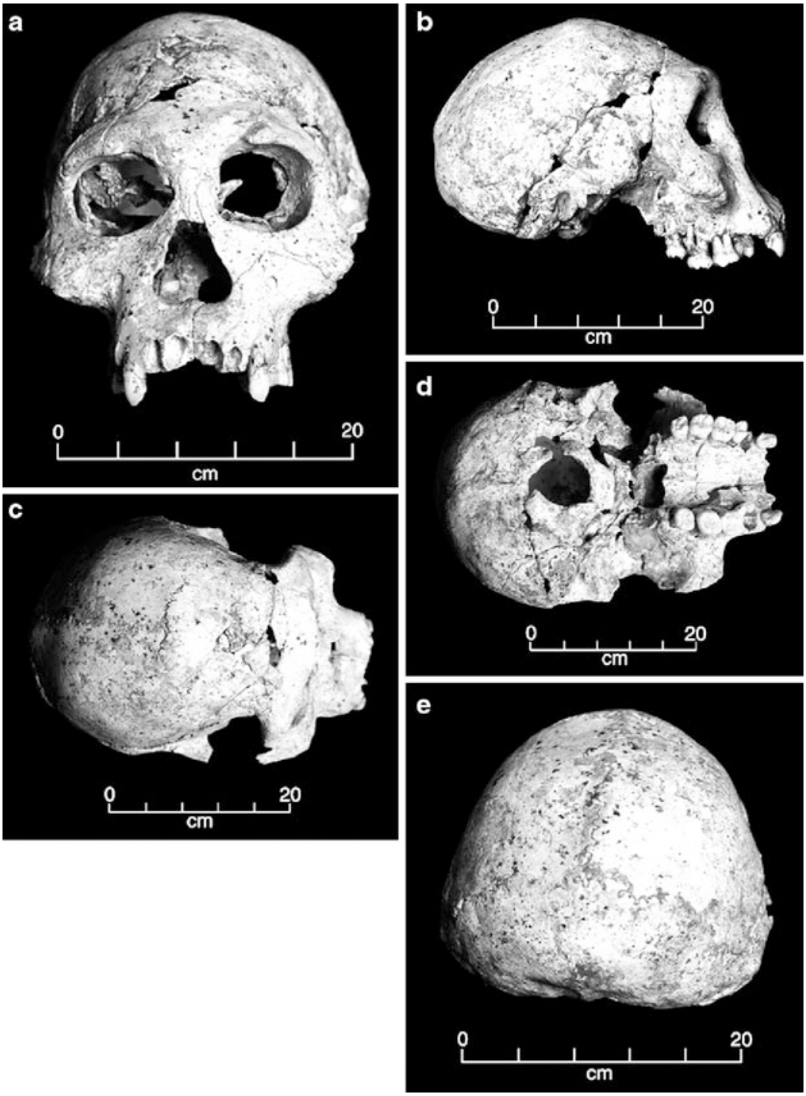

Fig. 6 Five views of the D 2700 cranium from Dmanisi (From Vekua et al. (2002), supplemental web data; Photos courtesy of David Lordkipanidze)

H. erectus by Henke (1995) and also by Bräuer and Schultz (1996), although these latter authors remarked that, oddly, this early mandible showed "progressive" features seen in geologically younger *H. erectus*. These early differences in interpretation foreshadowed a fairly wild taxonomic ride. Gabunia et al. (2000) reported the discovery of two crania (D 2280 and 2282; Fig. 3) close to the original site; they considered these comparable in size and morphology to Koobi Fora *H. ergaster*, although cranial volumes were somewhat smaller: 780 and 650 ml, respectively.

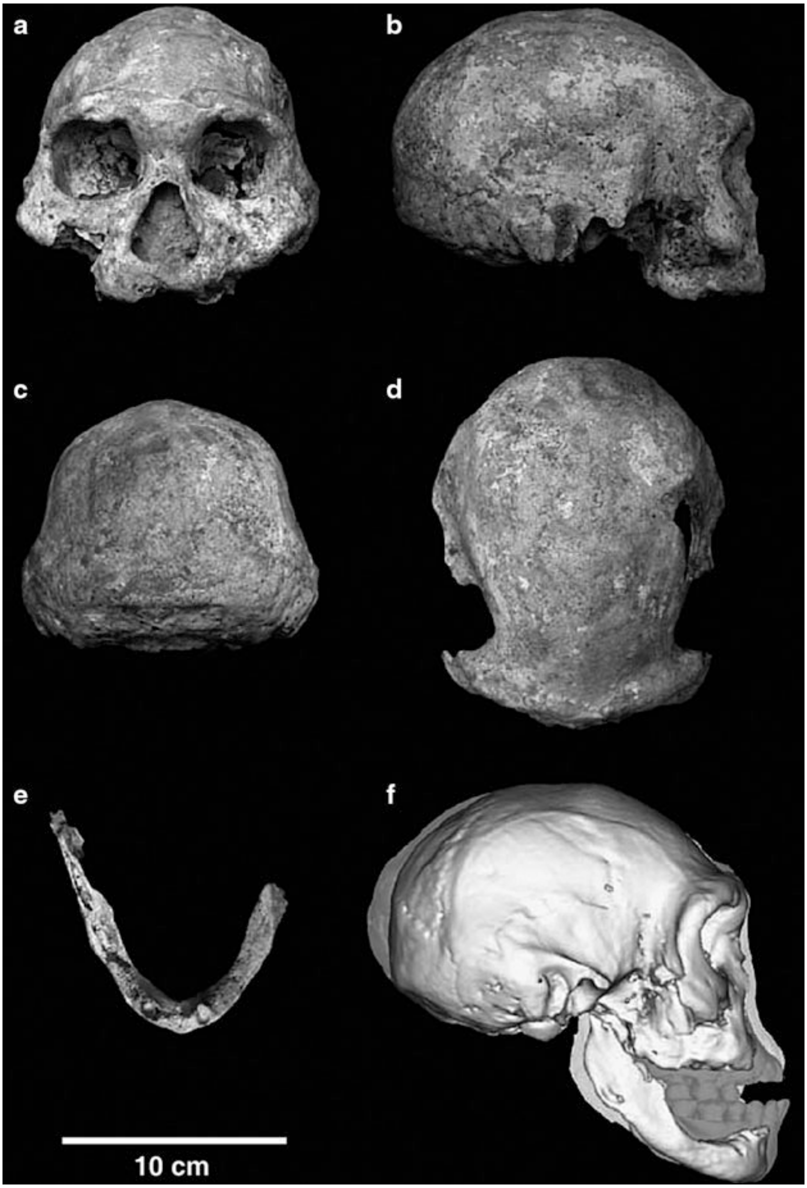

Fig. 7 The edentulous D 3444 cranium from Dmanisi. *Lower left*: mandible D 3900. *Lower right*: CT-based superimpositions by C. Zollikofer and M. Ponce de León of the Dmanisi skull D 3444/D 3900 on the D 2700/D 2735 and D 2282/D 211 specimens, to show contrasting silhouettes (From Lordkipanidze et al. (2005). Photos courtesy of David Lordkipanidze. Scale: 10 cm)

With the discovery in September 2000 of a very large and long mandible with highly worn teeth (D 2600; Fig. 5), the picture changed again. This mandible presented a marked contrast to D 211, but the Dmanisi team nonetheless concluded that all of the specimens belonged to a single highly sexually dimorphic species which they named *H. georgicus*, with D 2600 as its holotype (Gabounia et al. 2002). The gracile specimens D 211, D 2280, and D 2282 were considered to be female; and the robust D 2600 lower jaw was viewed as a male representative of this species. The group concluded that *H. georgicus* "preserves several affinities with *Homo habilis* and *Homo rudolfensis* … foretelling the emergence of *Homo ergaster*" (Gabounia et al. 2002, p. 245). But things did not stop there. Almost simultaneously, the team announced the discovery of an associated cranium and mandible, D 2700/D 2735 (Vekua et al. 2002; Fig. 6). Strikingly different from the crania discovered earlier, though also notably small-brained (600 ml), this excellently preserved specimen was said by its describers to bear resemblances to penecontemporaneous East African fossils. Abandoning the species *H. georgicus*, as well as the notion of *H. ergaster* as a separate entity, the Dmanisi team allocated D 2700/D 2735, and the rest of the hominid assemblage along with it, to *H. erectus*, while noting that they "are among the most primitive individuals so far attributed" to that expanded species (Vekua et al. 2002, p. 88).

During the 2002/2004 field seasons yet another associated cranium and mandible (D 3444/D 3900) were recovered at Dmanisi. The most remarkable aspect of this aged presumed male (Fig. 7) is that he had possessed just a single tooth at death and had evidently been largely edentulous for many years (Lordkipanidze et al. 2005). Although at least one recent chimpanzee is known to have survived a long time in an edentulous state, the Dmanisi team surmised that the individual must have "survived for a lengthy period without consuming foods that required heavy chewing … and/or by virtue of help from other individuals" (Lordkipanidze et al. 2005, p. 718), and suggested that this had significant implications for early hominid social structure. They also noted that the cranium had been found in close proximity to Mode 1 stone artifacts and to cut-marked animal bones. The authors refrained from commenting on the systematic implications of the new find; but in a review published soon afterward, Rightmire et al. (2006) reaffirmed their belief that the Dmanisi assemblage as a whole was a single "paleodeme" best placed within *H. erectus* (which to them subsumed *H. ergaster*), despite resemblances to *H. habilis* in brain volume and in some aspects of craniofacial morphology. Yet while they (Rightmire et al. 2006, p. 140) noted that, if the large D 2600 mandible could be accommodated within the rest of the Dmanisi hominid population, then "the appropriate nomen is *H. erectus georgicus*," they also pointed out that should the separate species status advocated by Gabounia et al. (2002) for the large jaw be "verified by new discoveries, then a subspecies other than *H. erectus georgicus* will have to be selected [for the remainder of the sample]."

The hoped-for new discovery, of the cranium matching the D 2600 jaw, was duly made at Dmanisi in 2005. Following a long agony of indecision, this complete and beautifully preserved specimen (D 4500) was finally published in 2013 (Lordkipanidze et al. 2013). The delay is quite understandable, for this fossil is quite unlike anything ever seen before. As one would have predicted from the large teeth and long tooth rows of the mandible, the new cranium possesses a large and highly prognathic face, which is hafted on to a remarkably small braincase with a volume of fractionally less than 550 ml. But while these attributes generally recall those of australopiths, Lordkipanidze and colleagues probably wisely refrained from associating their new specimen with any previously known early hominid taxon. Instead, they crammed it into *Homo erectus*, an assignment for which there is less than scant morphological justification. Declaring that the extraordinarily distinctive morphology of D 4500 "reflects variation between demes of a single evolving lineage" (Lordkipanidze et al. 2013, p. 330), the group concluded that "specimens previously attributed to *H. ergaster* are thus sensibly classified as a chronosubspecies, *H. erectus ergaster*" (Lordkipanidze et al. 2013, p. 330). And finally they took the astonishing step of reducing the entire Dmanisi hominid sample to the previously unknown status of a sub-subspecies, *Homo ergaster erectus georgicus*. If there is any substance whatever to this convoluted taxonomic judgment, systematists everywhere should be in mourning, because it effectively deprives morphology of any utility in systematics – and where are we left to go from there?

In any event, the contorted taxonomic journey of the Dmanisi hominids reflects the unusual morphologies that make it hard to fit them into established categories. And this journey is certainly not yet at an end. Even before the initial discovery of D 4500, Schwartz and Tattersall (2005) had already noted that the morphological heterogeneity in the Dmanisi assemblage made it difficult to recognize a single consistent morph at the site, irrespective of what this might have implied about species status. What is more, the lead geologist at Dmanisi, Reid Ferring (personal communication), reports that accumulation of the Dmanisi hominids might have taken place over the span of as much as a few hundred years. And if this is the case, there is no compelling reason (as there might be in the case of a catastrophic assemblage) to believe that only one hominid species is necessarily implicated in the fossil assemblage. Additionally, Schwartz and Tattersall observed that none of the Dmanisi material appeared to bear very close, i.e., systematically suggestive, resemblances either to any Asian fossils that had been described as *H. erectus* or to any African specimens allocated to *H. erectus* or to *H. ergaster*. Exactly how much systematic variety there is in this assemblage clearly awaits more study; but although the Dmanisi hominids most plausibly represent one or possibly more early departures from Africa hard on the heels of the origin of *Homo*, it is hard at present to point to craniodental morphologies that specifically unite them with any latest Pliocene or earliest Pleistocene African hominids yet known.

It is unknown with any certainty exactly what it was that allowed hominids to spread, for (presumably) the first time, out of the ancestral continent of Africa as far as Dmanisi. But since the Mode 1 stone tool assemblage at Dmanisi is remarkably primitive, and the brains of the hominid(s) there remained small, it seems most likely that the factor responsible was the acquisition of striding bipedality. As exemplified by WT 15000, this locomotor style was already present in *Homo ergaster*; and a partial postcranial skeleton from Dmanisi (putatively associated with the D 2700/D 2735) and postcranial bones from three other individuals are said to show “modern-human-like body proportions” (Lordkipanidze et al. 2007, p. 305). Still, the scientists who described these elements also noted a “surprising mosaic of primitive and derived features” (Lordkipanidze et al. 2007, p. 305); and it is clear that the last word on the Dmanisi postcranials–and indeed, on the assemblage as a whole–has yet to be written.

Conclusions

Homo ergaster is the designation of choice for the growing number of paleoanthropologists who believe that the fossils previously allocated to “African *Homo erectus*” are sufficiently different from the Asian type material of *H. erectus* to warrant assignment to a distinct species. Adoption of this nomenclature is a considerable improvement on our older understanding, certainly to the extent that it emphasizes that the Trinil fossil and others like it are quite highly autapomorphic and that Javan or at least eastern Asian *H. erectus* is thus most appropriately viewed as an indigenous and terminal regional species (or maybe even clade), rather than as an Old World-wide stage or grade in hominid evolution. Nonetheless, it remains true that to call the entire African rump of this Old World “*Homo erectus* grade” *H. ergaster*, is to brush a huge diversity of morphologies under the rug of one single species. Close examination of the morphologies displayed by the diversity of fossils that have at one time or another been referred to as “African *Homo erectus*” makes it evident that, while it is likely that all may be legitimately regarded as members of a single hominid clade, there is some diversity within it.

The KNM-ER 992 holotype mandible of *H. ergaster* appears to be matched morphologically by the OH 22 mandible from Olduvai as well as by another mandible (ER 3734) from Koobi Fora. But there seems to be no compelling reason to match these lower jaws with any of the cranial materials available, and certainly none to associate them with the iconic KNM-WT 15000 skeleton, the lower dentition of which is distinctly different in a whole host of characteristics. Clearly, there is a need for a detailed systematic reappraisal of the entire “African *Homo erectus*” = *Homo ergaster* group. Meanwhile, the recognition of a distinct *H. ergaster* clade at least serves to highlight the fact that the complexity of the hominid evolutionary story throughout the Old World in the Early–Middle Pleistocene was far greater than is implied by the inclusion of the entire group of fossils involved within the single hugely variable species *H. erectus*.

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Defining *Homo erectus*

Karen L. Baab

Contents

Abstract

Pithecanthropus (now *Homo*) *erectus* was first recognized as a species by Eugène Dubois in the 1890s from fossils at the Indonesian site of Trinil. Additional finds from Indonesia and then China expanded the morphological, geographic, and temporal bounds of this species, but it was not until 1960 that *H. erectus* was recognized in Africa. Since that time, *H. erectus* has become among the best sampled species in human evolution and has also come to include fossils from Eurasia and possibly South Africa. These fossils are united by a shared neurocranial shape and the presence of a large number of discrete traits. Yet, there is considerable variation among and within fossil assemblages, which has been interpreted within the framework of a long-lived and polytypic species

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K.L. Baab (✉)
Department of Anatomy, Midwestern University, Glendale, AZ, USA
e-mail: karen.baab@stonybrook.edu; klb714@gmail.com

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by some, and as indicative of multiple species by others. This chapter reviews the morphological features of the skull that serve to define *H. erectus*, as well as the extent and implications of variation across the fossil hypodigm. Sometimes the smaller and less derived African and Georgian fossils have been assigned to a separate species, *H. ergaster*. Yet, geometric morphometric analysis indicates that the degree of cranial shape variation for the entire sample (including African, Georgian, Indonesian, and Chinese fossils) is within the range of many single primate species, and the variation between Indonesian and Chinese fossils is of the same magnitude as that between African/Georgian and Asian fossils. Therefore, the single-species model for *H. erectus* cannot be rejected on the basis of cranial shape. However, not every fossil assigned to this species is a perfect fit, and some of the most recent additions to *H. erectus* expand the range of variation in directions that are unexpected based on established patterns of intraspecific variation. The analysis of shape has further confirmed that much of the cranial shape variation present within the species is partitioned among circumscribed temporo-geographic groups. Additional work is necessary to better understand the utility of discrete traits for systematic research and their distribution in the expanded Pleistocene *Homo* fossil record.

Introduction

Fossils assigned to *Homo erectus sensu lato* (*s.l.*) (including fossils from Indonesia, China, Africa and Georgia; Antón 2003; Rightmire et al. 2006; Baab 2008b) retain a broadly homogeneous cranial and postcranial *Bauplan* across an impressive geographic and temporal range. Yet, variation within this hypodigm is evident at both the population and individual levels. Disagreement concerning how this variation is interpreted is at the heart of the long-standing debate regarding whether the *H. erectus s.l.* fossil hypodigm represents a single species or multiple species. This chapter first outlines the geographic and temporal range of *H. erectus s.l.* with a particular emphasis on the historical development of this debate concerning alpha taxonomy. The three main hypotheses concerning *H. erectus s.l.* alpha taxonomy (the multiregionalism, the single-species model, and the multiple-species model) are then described. This is followed by a discussion of cranial discrete characters and aspects of cranial shape that have figured prominently in species definitions for *H. erectus s.l.*. Both the magnitude of cranial variation and the spatiotemporal patterns of variation are discussed, and the attribution of recently described fossils to *H. erectus* is examined against this background of variation.

Survey of Fossils Assigned to *Homo erectus sensu lato*

Many historical and geochronological surveys of *H. erectus s.l.* exist in the literature (e.g., Rightmire 1990; Antón 2003). For this reason, this chapter will briefly summarize the geographic and temporal span of this species, broadly defined, with particular emphasis on those fossils that are especially well preserved (and therefore morphologically informative), have played a key role in taxonomic and phylogenetic hypotheses, or are recent discoveries that are likely to be less well known to the reader.

Homo erectus was first discovered by Eugène Dubois on the Indonesian island of Java, which subsequently became a source of many additional fossils usually assigned to this species. Many of the best-known *H. erectus* fossils derive from the sites of Trinil (including the type specimen, Trinil 2; Dubois 1894) and the Sangiran Dome (including the most complete cranium of Asian *H. erectus*, Sangiran 17). A series of lesser-known fossil calvaria and fragments of faces have also been recovered since the late 1970s from Sangiran Dome localities, including some of the oldest Indonesian fossils (Sangiran 27 and 31, Bpg 2001.04) (Jacob 1980; Sartono 1982; Indriati et al. 2008; Zaim et al. 2011) and the remarkably well-preserved Skull IX (Tjg-1993.05) calvarium (Arif 2005; Kaifu et al. 2011). The *H. erectus* fossils from these two sites range in age from more than 1.5 to ~1.0 Ma (Larick et al. 2001). Further east, the juvenile cranium from Modjokerto was recently confirmed to be from the Sangiran Formation (Huffman 2001; Huffman et al. 2005, 2006), which was dated at Sangiran to >1.5 Ma by Larick et al. (2001). The sites of Ngandong, Sambungmacan, and Ngawi together have yielded more than a dozen complete or partial calvaria, the most recent of which was discovered in 2001 (Sambungmacan 4), (Baba et al. 2003b). The dating of Ngandong has been controversial, and estimates have ranged from Early to Late Pleistocene. The very young ages of 35–50 ka for the Ngandong and Sambungmacan 1 locality (Swisher et al. 1994) appear to be inaccurate, and a more recent estimate for Ngandong is a Middle Pleistocene age of ~546 Ma (Indriati et al. 2011). The lack of provenance for the Sambungmacan and Ngawi fossils precludes accurate date estimates, but they are morphologically closer to Ngandong than to the Sangiran/Trinil series (Baab 2010). The geographic range of Indonesian *H. erectus* was recently expanded westward to the site of Cisanca where a single incisor was recovered (Kramer et al. 2005).

The most productive of the Chinese sites is the famous Zhoukoudian Cave, from which a series of well-preserved calvaria were recovered, mostly in the 1930s. The consensus during the 1980s was that hominin activity at Zhoukoudian Cave Locality 1 was from ~500 to 230 ka (Zhao et al. 1985). Recent estimates are older: analysis of radioactive ^{26}Al and ^{10}Be in the cave sediments indicated an age of ~770 ka for the oldest hominin fossil-bearing stratum (Shen et al. 2009), while the youngest fossil was probably 400–500 ka based on ^{230}Th/^{234}U dating of cave speleothems (Shen et al. 2001). Additional Chinese *H. erectus* fossil sites include Yiyuan, Nanjing (Tangshan), Hexian, Gongwangling (Lantian), Chenjiawo, Yunxian, and Yuanmou (Li and Mei 1983; Wu et al. 1989; An et al. 1990; Yan 1993; Chen et al. 1997; Grün et al. 1998; Zhao et al. 2001; Liu et al. 2002; Wang et al. 2002). Many of these sites appear to be of Middle Pleistocene age, although ages in excess of 0.9 Ma have been proposed for Yunxian (0.936 Ma; de Lumley et al. 2008), Gongwangling (~1.15–1.2 Ma; An and Ho 1989; An et al. 1990; Zhu et al. 2003), and Yuanmou (~1.7 Ma; Li et al. 1976; Qian and Zhou 1991;

Huang and Grün 1998; but see Hyodo et al. 2002; Zhu et al. 2003). Both the Yiyuan and Nanjing fossils bear strong similarities to the Zhoukoudian sample, but the Hexian cranium is distinct from this group (Lu et al. 1989; Etler 1996; Kidder and Durband 2004a; Liu et al. 2005). The Gongwangling and Yunxian cranial fossils suffered considerable postmortem damage, and while both are usually allied with *H. erectus*, the latter are sometimes grouped with later archaic *Homo* (Li and Etler 1992; Wu and Poirier 1995; Zhang 1998; Brown 2001).

Both cranial and postcranial fossils attributed to *H. erectus* have been recovered from East, South, and North Africa. Significant fossil discoveries from East Africa were made at Olduvai Gorge, including the robust OH 9 skull and the smaller OH 12, and in the Turkana Basin of Kenya, including the type specimen of *H. ergaster* (the mandible KNM-ER 992), two crania often assigned to *H. ergaster* (KNM-ER 3733, 3883), and the remarkably complete juvenile skeleton, KNM-WT 15000. Fossils from Olduvai Gorge and the Turkana Basin fall between 1.9 and 1.2–1.02 Ma (Feibel et al. 1989; Hay 1990; Brown and McDougall 1993; Tamrat et al. 1995). The oldest fossil assigned to *H. erectus* is a fragment of occipital bone (KNM-ER 2598) dated to 1.88–1.9 Ma (Feibel et al. 1989; but see White 1995) and attributed to *H. erectus* on the basis of the thickness of the bone and the presence of an occipital torus (Wood 1991). This time range overlaps the Indonesian time frame but also extends it further into the past. More recent East African discoveries include two small specimens, an older subadult from Ileret, Kenya (KNM-ER 42700), and a fragmentary calvarium from Olorgesailie, Kenya (KNM-OL 45500), dated to 1.5–1.6 and 0.90–0.97 Ma, respectively (Leakey et al. 2003; Potts et al. 2004). If correctly assigned, these extend the size range of *H. erectus* in Africa. Isolated postcrania are often referred to *H. erectus*, such as the KNM-ER 3228, OH 28, and BSN49 pelves from Kenya, Tanzania, and Ethiopia, respectively, but these attributions are hard to confirm. Two younger fossils from Bouri, Ethiopia (the Daka cranium), and Buia, Eritrea (the Buia cranium) span the time period of 0.8–1.0 Ma and exhibit more derived traits than other African *H. erectus*. In fact, doubts have been raised about the inclusion of Buia in *H. erectus* (Antón 2003). A pelvis recovered from Gona, Ethiopia, dated to 1.4–0.9 Ma has been assigned to *H. erectus*, and the SK 847 (~1.7 Ma; Brain 1993) partial cranium from South Africa is also sometimes assigned to this species (originally *Telanthropus capensis*).

A series of sites in Middle Pleistocene North Africa, Tighinif (Ternifine), Salé, Thomas Quarries, and Sidi Abderrahman, have yielded mandibular and cranial fossils sometimes assigned to *H. erectus*. The Tighenif fossils were initially assigned to *Atlanthropus mauritanicus* (Arambourg 1954) but later to *H. erectus*. However, these fossils are now more often attributed to later *Homo*. Other African fossils previously assigned to *H. erectus*, including Salé, Ndutu, Bodo, and Kabwe (Broken Hill), are now considered part of the *H. heidelbergensis* hypodigm (sensu Rightmire 1998b; 2008; 2013).

Five crania, some associated with mandibles, and many postcranial elements have been recovered at the Eurasian site of Dmanisi, Georgia, from 1.77 Ma deposits (Gabunia et al. 2000; Simpson et al. 2008), but artifacts have been found in deposits as old as 1.85 Ma (Ferring et al. 2011). A combination of *H. erectus*-like traits as well as plesiomorphic features more often observed in earlier taxa like *H. habilis* led some to classify these fossils as *H. erectus* (e.g., Rightmire et al. 2006), but others to create a new taxon, *H. georgicus* (Gabounia et al. 2002; de Lumley et al. 2006). A partial calotte from Kocabaş, Turkey, was recently assigned to *H. erectus*, mostly on the basis of its frontal bone anatomy (Kappelman et al. 2008; but see Stringer 2012). Additional European fossils previously considered to be *H. erectus* are now more commonly assigned to later *Homo* taxa: Ceprano, Petralona, Arago, Bilzingsleben, and Vértesszöllös.

Homo erectus sensu lato Alpha Taxonomy

A Historical Overview

The early discoveries of *H. erectus* in Asia initially included several distinct genera: *Pithecanthropus*, *Meganthropus*, and *Sinanthropus*, many of which included multiple species. This early plurality was followed by compression of these taxa into fewer, more inclusive taxa. For example, von Koenigswald and Weidenreich (1939, p. 928) concluded that the remains from Java (specifically Trinil, Sangiran, and Kedung Brubus) and China (Zhoukoudian) "were related to each other in the same way as two different races of present mankind" and Weidenreich (1940) included them as subspecies within *H. erectus*. Similarly, Mayr (1950) sunk both *Pithecanthropus* and *Sinanthropus* into *H. erectus* in his highly influential 1950 publication. Similar concatenations occurred with the South and North African material. *Telanthropus capensis* was first moved into *Pithecanthropus capensis* (Simonetta 1957) and then *H. erectus* (Robinson 1961). *Atlanthropus mauritanicus* was sunk into *H. erectus* as early as 1964. Leakey, Walker, and colleagues assigned African fossils from Olduvai Gorge and the Turkana Basin to *H. erectus* throughout the 1960s–1980s (Leakey 1961, 1976; Walker and Leakey 1978; Brown et al. 1985; Leakey and Walker 1985). Detailed morphological analysis led Santa Luca (1980) to conclude that the fossil assemblage from Ngandong (originally *Javanthropus soloensis*) should be subsumed within the *H. erectus* species. Therefore, by the mid-1980s *H. erectus s.l.* was a broadly configured species that included representatives as old as 1.9 Ma and as young as 0.5 or 0.4 Ma and occupying sites as far south as South Africa and as far east as Indonesia and China. Additional fossils from these major regions have been added subsequently, and the geographic range was expanded with the addition to *H. erectus s.l.* of the fossils from Dmanisi and possibly Turkey. A small minority of workers have gone even further, moving all of these *H. erectus s.l.* specimens into *H. sapiens*, which would also include mid-Pleistocene *Homo* fossils and early and recent modern humans, and a recent study questioned whether early *Homo* species might also be subsumed within *H. erectus* (Lordkipanidze et al. 2013). However, many workers have continued to recognize a multiplicity of species and even genera for the same fossil sample.

Systematics Controversy

This debate is not simply a matter of semantics as alpha taxonomies provide the raw material for analyses of species diversity and rates of diversification, and influence views of intraspecific, including sexual, variation. The widespread disagreement regarding Pliocene–Pleistocene *Homo* systematics is related to many factors, including fundamental differences in how species are defined theoretically and operationally and the underlying phylogenetic scenarios to which they are inextricably linked (e.g., compare Tattersall 1986; Wolpoff et al. 1994). Evolutionary/taxonomic scenarios range from the well-known regional continuity model at one extreme to the "bushy tree" model at the other. Most workers adhere to one of two intermediate positions, which correspond to a single, polytypic species model or a two-species model. Each will be described briefly below, followed by a discussion of how morphology is interpreted under these different models.

Weidenreich (1943, 1951) argued for a more or less unilinear view of hominin evolution which recognized successive evolutionary stages or grades, defined morphologically by shared set of features. He further viewed "racial" or geographic groups of modern humans as having their roots in the archaic taxa that preceded them in those same regions. Weidenreich's early application of multiple genus and species names represented a convenient way to refer to different samples of fossils rather than a formal taxonomy that reflected his phylogenetic hypothesis (Mayr 1950). This is particularly clear in his 1951 monograph on the Ngandong fossils where he states:

> As to nomenclature, in general, I believe that all the hominids now known belong morphologically to a single species, and therefore I regard subdivisions expressed in terms of fixed taxonomy as a matter of secondary concern. (Weidenreich 1951, p. 226)

More recent standard bearers for this multiregional evolutionary scenario still adhere to a gradistic view of human evolution but place more emphasis on gene flow among regions (Thorne and Wolpoff 1981; Wolpoff et al. 1984, 1994; Hawks et al. 2000). The gradual nature of morphological transitions among grades has led to the proposal that fossils traditionally assigned to *H. erectus s.l.* should instead be subsumed into a single evolving *H. sapiens* species (Jelínek 1982; Wolpoff 1984; Wolpoff et al. 1984, 1994; Curnoe 2006).

A contrasting perspective is that *H. erectus* is a "real" species (including all or nearly all of the fossils described above) that is morphologically distinct from other species (Howell 1978; Howells 1980; Rightmire 1984, 1986, 1990, 1998a, 2006; Harrison 1993; Antón 2003; Baab 2008b). In this context, *H. erectus* is morphologically differentiable from both early *Homo* (Rightmire et al. 2006) and later *Homo* (Rightmire 2013). Under the single-species model, variation is viewed as the norm for a widespread polytypic species. In the words of Rightmire (1998b, p. 220):

> . . .it is interesting that the Asian populations apparently are more specialized in the sense of exhibiting a higher incidence of some morphological characters associated with cranial robusticity. These traits are subject to geographic variation and do not mark a species boundary, but they may nevertheless delimit groups that had different evolutionary fates.

Antón (2003), adopting Jolly's (2001) suggestion, proposed that anatomically distinct geographic variants be viewed as parapatric allotaxa – neighboring populations that are at once in possession of the same basic anatomy and able to hybridize, yet distinguishable from one another. Phylogenetically, Rightmire (1998b) proposed that some populations of *H. erectus* in Africa or western Asia were ancestral to later *Homo* species, a speciation event that occurred by the Early Pleistocene. Other populations, particularly in eastern Asia, survived until more recently but eventually went extinct and were replaced by dispersals of more derived species.

The rise of cladistic thinking in anthropology encouraged a focus on autapomorphies in species definitions (Andrews 1984; Stringer 1984; Wood 1984, 1991; Tattersall 1986; Groves 1989). The higher frequency of autapomorphic traits in the Asian fossils, such as thicker cranial bones, midline and coronal keeling, an angular torus, and a fissure between the mastoid process and the petrosal crest of the tympanic, provided the basis of a species definition for *H. erectus sensu stricto* (*s. str.*) that excluded either all African fossils (Andrews 1984; Stringer 1984) or at least the Koobi Fora portion of the African record (Wood 1984, 1991, 1994) (Note that the African record at that time did not yet include fossils such as KNM-ER 42700, KNM-OL 45500, and Daka.). Moreover, synapomorphies were identified in the Koobi Fora remains and *H. sapiens* that were lacking in *H. erectus* (Wood 1992). This distribution of autapomorphies and synapomorphies suggested the following phylogenetic scenario to Andrews (1984, p. 172):

> . . .my provisional interpretation of the evidence would be that the African skulls formerly attributed to *erectus* would have been close to the line leading to *sapiens* and that the Asian *erectus* was some way removed from this lineage.

Hence, *H. ergaster* was embraced as a species comprised Pliocene–Early Pleistocene African fossils possibly ancestral to both a lineage of more derived *Homo* (*H. heidelbergensis s.l.*) and to *H. erectus s. str.*, itself an evolutionary dead end.

Even more speciose taxonomies assume a greater number of cladogenic events. For example, a three-species model comprised *H. erectus s. str.*, *H. ergaster*, and *H. georgicus* is premised on the latter having diverged from early *Homo* prior to the emergence of *H. ergaster* (Gabounia et al. 2002; de Lumley et al. 2006; Martinón-Torres et al. 2008). The relationships among these three species, however, remain unclear. Other researchers embrace an even bushier tree during this time period, arguing that closely related species are often hard to distinguish on the basis of hard tissue anatomy alone, and therefore diagnosable units in the fossil record most likely represent distinct species (Tattersall 1986, 1992). Tattersall and Schwartz have identified many "morphs," which Tattersall (1992, p. 345) has previously equated with "at the very least. . .genetically disjunct species," even within single sites and restricted time periods (e.g., Koobi Fora, Schwartz and Tattersall 2003; Dmanisi, Schwartz and Tattersall 2005). However, true species diagnoses and nomenclature are lacking, and a phylogenetic hypothesis linking these taxa together has not yet been articulated.

Defining *Homo erectus sensu lato*

The morphological definition of *H. erectus s.l.* offered below is a combination definition (sensu Wood 1984) that includes plesiomorphic, synapomorphic, and possibly autapomorphic characters that together are found only in this species, even if individual features evince a broader taxonomic distribution. This list is general in nature, and there is a well-documented variation across populations and individuals in the expression of these traits (see below), consistent with a polymorphic species (Rightmire 1986, 1990; Turner and Chamberlain 1989; Antón 2003). Cranial features have weighed most heavily in taxonomic debates because cranial remains dominate the *H. erectus* fossil sample. This discussion will therefore be biased in favor of cranial morphology. There are a number of traits which are common (but not necessarily ubiquitous) in the broadly defined *H. erectus* species, which can be roughly divided into discrete characters and shape characters. For this discussion, "discrete" traits are locally restricted features not easily measured with standard morphometric tools, whereas shape traits refer to large-scale features that are more amenable to measurement ("metric" traits). Some characters could be accommodated in either category (e.g., form of the supraorbital region), and their categorization is arbitrary.

Many of the discrete characters that serve to define *H. erectus s.l.* are termed cranial superstructures and represent localized hypertrophies of the cranial bones in the form of keels, tori, and crests. Keeling often occurs along the midsagittal suture, the median plane of the frontal bone, and the coronal sutures, and may be associated with a bregmatic eminence (Fig. 1). Among the most prominent of the cranial superstructures are the occipital torus and the supraorbital torus. The first traverses the occipital bone at the junction of the occipital and nuchal squamae, and its inferior surface is sometimes excavated by nuchal musculature such that it overhangs the nuchal plane. The latter is anteriorly projecting, may be straight along both its anterior and superior borders, and is usually found in conjunction with a supratoral sulcus. The angular torus is located at the posterior extent of the temporal lines as a raised arc of bone on the parietal near the mastoid notch. Mastoid, supramastoid, and suprameatal crests may be present on the lateral aspect of the temporal bone, a juxtamastoid eminence may form medial to the mastoid process, and there are sometimes postcondylar tuberosities posterior to the occipital condyles.

Additional discrete traits that are not superstructures include a mastoid fissure (a fissure between the mastoid process and the tympanic tube) and a narrowing of the glenoid cavity into a fissure between the entoglenoid pyramid and the tympanic plate. There is no sphenoid spine. The petrotympanic crest is often thick with a petrous crest anterior to the stylomastoid foramen and styloid pit and a projecting processus supratubarius located at its medial end near the carotid canal. *H. erectus* is frequently described as lacking both a styloid process and a vaginal sheath, though this is variable. The petrous pyramid is more sagittally oriented than in modern humans. The mastoid process is often described as small, and the tip may be inclined medially with a flattened posterior surface

Fig. 1 *Homo erectus* cranial morphology and variation. *Homo erectus* cranial morphology from several perspectives (from *top* to *bottom* and *left* to *right*): *left lateral* (Sangiran 2), posterior (Dmanisi 3443 – cast), superior (Zhoukoudian 3 – cast), inferior (OH 9), and anterior (KNM-ER 3733). Note many of the key *H. erectus* cranial traits discussed in the text, including the long and low midsagittal profile, angled occipital bone, flat frontal bone, postorbital constriction, well-developed supraorbital torus with a posttoral sulcus, occipital torus, midline keeling, maximum breadth positioned low on the vault, a heavily constructed cheek region, a fissure between the tympanic tube and the entoglenoid process, and the processus supratubarius at the medial end of the tympanic plate. Photographs by K.L. Baab (Turkana image with permission of the National Museum of Kenya)

(Rightmire and Lordkipanidze 2009), but again, this is not universal. Inion and endinion are often vertically separated, and inion and opisthocranion are coincident (or nearly so) (Dubois 1924; Weidenreich 1943, 1951; Howell 1978; Howells 1980; Santa Luca 1980; Rightmire 1984, 1990; Wood 1984, 1991; Antón 2002, 2003). A final *H. erectus* feature that is not easily classified as either a cranial shape or a discrete trait is that of thickened cranial vault bones (Kennedy 1991; Brown 1994; but see Balzeau 2006).

Aspects of cranial shape traditionally used to define *H. erectus* include a low and elongated cranial vault when viewed laterally, marked postorbital constriction, maximum cranial breadth across the angular torus or supramastoid crests, a high occipital/parietal arc ratio, flattened frontal squama and parietal bones, a low and flat temporal squama (in contrast to an arched squama), an acutely angled occipital bone in the sagittal plane, a longer nuchal than occipital plane, an unflexed cranial base, and a more sagittally oriented petrous temporal (Fig. 1) (Dubois 1924;

von Koenigswald and Weidenreich 1939; Weidenreich 1943, 1951; Le Gros Clark 1964; Howells 1980; Maier and Nkini 1984; Wood 1984; Rightmire 1990; Antón 2003). *Homo erectus* is described as having a wide midface, a massive cheek, a prominent nasal saddle, and a wide nasal aperture (Rightmire and Lordkipanidze 2009).

Do the preceding characteristics of *H. erectus s.l.* serve to delineate this species from other closely related species? In general, workers have focused on differentiating early African *H. erectus* (*H. ergaster*) from Asian *H. erectus* (*H. erectus s. str.*) rather than delineating *H. erectus* from early *Homo* (*H. habilis* and *H. rudolfensis*). That said, early *Homo* may have thinner cranial bones and fewer cranial superstructures than *H. erectus*, although their low frequency in the Koobi Fora *H. erectus* diminishes this distinction. Of the rather large number of traits that characterized *H. erectus s.l.* listed above, Rightmire (1990) singles out nine that are derived in *H. erectus s.l.* relative to earlier species, including a midline keeling on the frontal bone, an angular torus, a fissure between the entoglenoid process and the tympanic tube, and a prominent petrotympanic crest with a processus supratubarius. Turner and Chamberlain (1989) identified five additional features that differentiate *H. erectus* from early *Homo*, including broader nasal bones with a distinct nasal spine and a shorter temporal fossa. Antón (2004) highlighted derived features of the *H. erectus s.l.* face, such as a broad interorbital region that is convex side to side and a more convex lateral malar.

At the other end of the phylogenetic bracket, many classical systematic treatments focused on differentiating *H. erectus* from *H. sapiens* rather than taxa now recognized as morphologically and chronologically intermediate, such as *H. heidelbergensis*, *H. rhodesiensis*, and *H. antecessor*. Modern human crania are easily differentiable from *H. erectus* because of their globular neurocrania (including a vertical forehead, parallel vault walls, separation of inion and opisthocranion, and greatest breadth across the parietals), thin cranial bones, smaller and more orthognathic faces, and distinct chins. Fossils assigned to the Middle Pleistocene taxa mentioned above are more difficult to distinguish from *H. erectus* because they often express traditional *H. erectus* traits, such as sagittal keeling, angular tori, thick cranial bones, and an occipital torus. However, these fossils generally have larger endocranial volumes, higher vaults, more vertical cranial vault walls, less sharply angled occipitals, and even more pronounced supraorbital tori than *H. erectus*. Additional features identified by Rightmire (2008) include a thinner tympanic plate and the presence of a sphenoid spine as well as a more arched temporal squama and longer occipital scale in *H. heidelbergensis s.l.* Some European *H. heidelbergensis* specimens also exhibit incipient Neanderthal traits.

Cranial shape can also be characterized and analyzed via geometric morphometric analysis of three-dimensional (3D) landmark data. Fifty-five landmarks, capturing overall neurocranial shape, were analyzed via principal components analysis (PCA) after superimposing all landmark configurations using standard Procrustes-based procedures (Gower 1975; Rohlf and Slice 1990) (chapter "▶ Virtual Anthropology and Biomechanics," Vol. 1). The superimposition process scales all individuals to the same overall size, so that only shape is analyzed. Unfortunately, preservation issues limited the sample of early *Homo* to

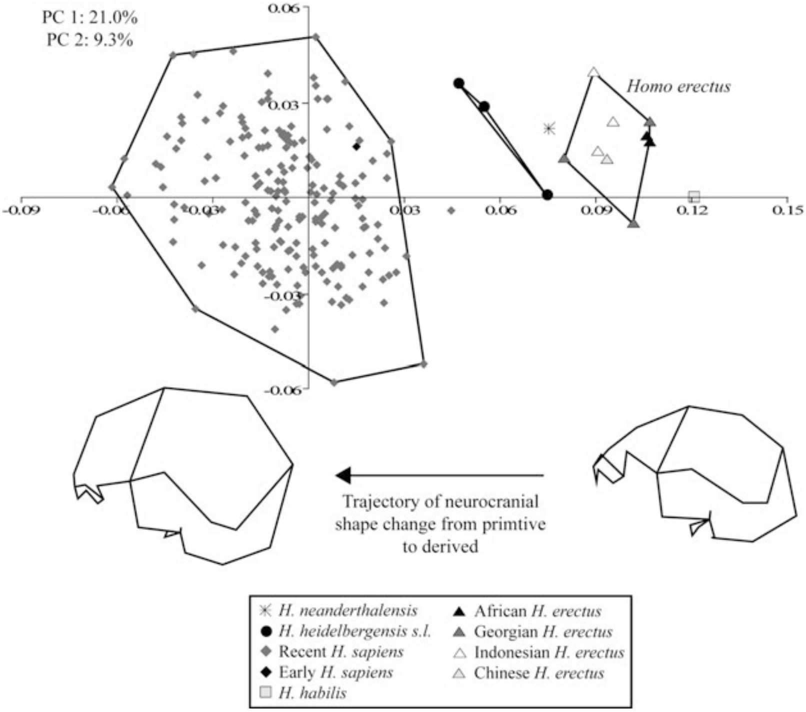

Fig. 2 *Homo erectus* neurocranial shape in a broader comparative context of extinct and extant *Homo* species. A comparative analysis of cranial shape using principal components analysis of 3D cranial landmarks from *Homo erectus* and other closely related *Homo* species. The first two principal components are figured. The first component captures the contrast in neurocranial shape between archaic *Homo* species and *H. sapiens*. *Homo erectus* is intermediate between the two extremes, represented by *H. sapiens* and *H. habilis*, but closer to the latter. Its distribution in morphospace also borders on mid-Pleistocene *Homo*. The wireframes illustrate shape differences along the first component: the high-scoring archaic taxa have a low neurocranial profile in contrast to the more globular shape of the cranial vault in modern humans. Other differences include the low position of greatest cranial breadth, more marked postorbital constriction, and pronounced browridge in the extinct species, whereas modern humans have more vertical cranial vault walls, reduced constriction, and a gracile supraorbital region

a sole *H. habilis* cranium (KNM-ER 1813). The *H. erectus* sample includes representatives of most major geographico-temporal groups (Sangiran, Ngandong, Sambungmacan, Zhoukoudian, Koobi Fora) but excludes some fossils due to incomplete preservation (e.g., KNM-WT 15000 and OH 9) or because their status as *H. erectus* remains unclear (e.g., KNM-ER 42700 and Daka). The first axis preserves a basic archaic to derived trajectory anchored on one end by *H. habilis* and on the other by *H. sapiens*, with *H. erectus s.l.* and Middle Pleistocene *Homo* specimens, including Neanderthals and what has been broadly referred to as *H. heidelbergensis*, arrayed between them (Fig. 2). The *H. erectus* sample overlaps or abuts the early end of the time range for *H. heidelbergensis*, but the two samples

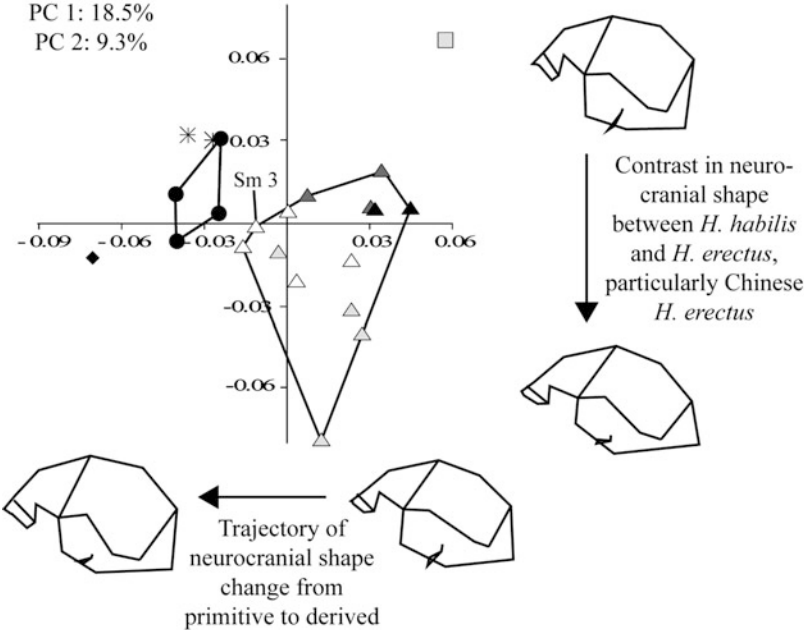

Fig. 3 *Homo erectus* neurocranial shape compared to fossil *Homo* species. A comparative analysis of neurocranial shape using principal components analysis of 3D cranial landmarks from *Homo erectus* and other closely related *Homo* species, excluding recent *H. sapiens*. This analysis features a more restricted set of landmarks but larger fossil sample than Fig. 2, but a similar pattern of archaic to derived neurocranial shape differences is apparent on PC 1 as seen in Fig. 2. The second component emphasizes how *H. habilis* (KNM-ER 1813) and Chinese *H. erectus* contrast with one another and with the remainder of the sample. *Homo erectus* again occupies a unique region of morphospace compared to its congeners. Sambungmacan 3 is labeled to emphasize how its more globular cranial vault converges on more derived *Homo* species. Legend is the same as in Fig. 2

analyzed here are distinct from one another in their cranial vault morphology. A similar pattern is evident in an analysis of a more restricted set of 39 neurocranial landmarks limited to just fossils but also demonstrates that the Chinese sample (PC 2) (Fig. 3) and the Indonesian sample (PC 3; not illustrated) are divergent from this main branch. The lack of overlap between *H. erectus* and closely related *Homo* species suggests that this species is distinct in terms of cranial shape, although larger samples of both earlier and later *Homo* are necessary to confirm this.

Variation in *Homo erectus sensu lato*

The preceding description of *H. erectus* obfuscates geographic, temporal, allometric, and interindividual (including sexual) variation within the sample. Indeed, many of the features described are not present in all members of the species and may in fact serve to delineate among samples from different regions or from different time periods. Perhaps the biggest stumbling block in studying *H. erectus* systematics is distinguishing between intra- and interspecific variations. Are differences between fossils from Koobi Fora and West Turkana (and perhaps Olduvai Gorge and Dmanisi) and those from Asia indicative of a cladogenic event? Or could this variation be attributed to temporal and spatial variation in a widespread and temporally deep species?

Magnitude of Variation

While many workers adhere to some version of the biological species concept, this cannot be directly applied to the study of paleospecies. A common "work-around" is to use extant species as a yardstick against which to gauge the degree of morphological variability in a fossil sample. The underlying assumption is that morphological variability is the outcome of a shared gene pool and membership in a single evolving lineage. Therefore, a fossil sample exhibiting more variation than the extant analogs may contain members of multiple species. However, this alone is insufficient to falsify the null hypothesis of a single species as issues unique to the fossil sample, such as greater temporal depth or greater sexual dimorphism, may give a false signal of excessive variation (Kelley and Plavcan 1998).

Explicit tests of the single-species hypothesis based on the degree of metric variability in *H. erectus s.l.* have generally supported a single-species model (Kramer 1993; Bilsborough 2000; Villmoare 2005), but this result is not universal (Terhune et al. 2007). Interestingly, analyses confined to just the Dmanisi sample have also come to contrasting conclusions: variations in cranial dimensions and endocranial capacity were within the range of a single species (Macaluso et al. 2004; Lee 2005), but size and shape dimorphisms of the mandibles were excessive for a single species (Skinner et al. 2006). A recent analysis which includes all five skulls found that variation was within expectations for demes of chimpanzees and bonobos and for a worldwide modern human sample (Lordkipanidze et al. 2013). The borderline nature of this result was reinforced by Baab (2008b) who found that variation in the neurocranial shape of *H. erectus* (captured by 16 3D landmarks) was more variable than *H. sapiens* and both chimpanzee species, less variable than *Pongo* and *Gorilla* species, and most comparable to the geographically disperse *Papio hamadryas* species (including representatives of six subspecies) and the *Macaca fascicularis* species group (including four species). Although the results were somewhat ambiguous, a single-species model was not rejected given the overlap in cranial vault variability between *H. erectus s.l.* and several extant primate species (or even species groups), especially in light of the greater geographic and temporal depth in the fossil sample.

The degree of variation among regional/temporal subsamples can also be assessed and compared to variation documented within and between extant species.

The degree of neurocranial shape differentiation observed between *H. ergaster* and *H. erectus s. str*. as defined by Wood (1991) (where the former is restricted to the Koobi Fora fossils and the latter includes both Asian fossils and OH 9) is less than the distance between strictly geographic or temporal subsets of fossils (Baab 2008b). Although not reported in the original study, the distance between Chinese and Indonesian samples exceeds that seen in the African/Georgian vs. Asian comparisons. Villmoare (2005) also evaluated distances between African and Asian *H. erectus s.l.* based on craniometrics and discrete traits relative to distances between regional groups of *H. sapiens*. He found that metric variation in the fossil sample did not exceed that found in modern humans but that variation in discrete characters did exceed that observed among regional groups of modern humans.

Pattern of Variation

A second and equally crucial piece of the puzzle is understanding how variation is patterned within this sample. One current challenge is parsing out variation due to different sources. For example, temporal trends in cranial shape evolution run largely parallel to allometric variation in this taxon as cranial capacity has increased over time in *H. erectus s.l.*, resulting in changes to cranial form. Therefore, to a large extent the effects of time and size are confounded in this sample. Despite these caveats, some generalizations can be made, and certain patterns are apparent. In addition to the discussion of variation below, readers are also referred to Antón (2003) and Baab (2007) for additional details pertinent to variation in *H. erectus s.l.* cranial morphology.

It was the higher frequency of certain discrete traits in the Asian fossils that initially prompted researchers to question the inclusion of the early African fossils in *H. erectus s. str*. Traditionally, these traits include thicker cranial bones, an occipital torus that is continuous with the angular torus and mastoid crest laterally, a supramastoid crest, a straighter frontal torus in anterior and superior views with a continuous posttoral sulcus, a midline keeling on the frontal bone and sagittal suture, a mastoid fissure, and a fissure between the tympanic plate and the entoglenoid pyramid (e.g., Andrews 1984; Stringer 1984; Wood 1984; Antón 2003; Villmoare 2005). The general lack of cranial superstructures in the African fossils is mirrored in the Georgian fossils (Antón 2003).

However, two objections have been raised to this observation of geographic differentiation: (1) many of these features appear to have a broader distribution in African and Georgian *H. erectus* and even outside of *H. erectus* (Rightmire 1986; Turner and Chamberlain 1989; Bräuer 1990; Kennedy 1991; Bräuer and Mbua 1992; Brown 1994; Villmoare 2005; Rightmire et al. 2006), and (2) these traits more accurately describe the Zhoukoudian (and other Chinese) fossils than the Indonesian fossils (Antón 2002). A further complication relates to the subjectivity of describing complex and often continuously varying morphology. For example, Antón (2004) describes KNM-ER 3733 as having "an apparently continuous, concave supratoral sulcus that rises relatively steeply to meet the frontal squama" (see also Rightmire 1990), whereas Wood (1984, 1991) argues that this same specimen lacks a well-defined supratoral sulcus.

Questions have been raised regarding the independence of these traits. Hublin (1986, 1987) put forth the interesting proposal that cranial superstructures (which comprise the majority of the proposed *H. erectus* autapomorphies) are developmentally integrated and are not therefore independent from one another. He specifically ties their development to thick cortical bone as cranial superstructures are localized hypertrophies of the outer layer of cortical bone (with the exception of the supraorbital torus which also involves the diploe). The endocrine factors responsible for cortical bone deposition may therefore also influence the development of these superstructures. Empirical evidence has been garnered both in support (Hublin 1987) and opposition of this idea (Balzeau 2013). In addition, both Lahr and Wright (1996) and Baab et al. (2010) found that cranial robusticity was integrated with cranial form in modern humans, and cranial superstructure expression may therefore relate to cranial size and shape in *H. erectus*. If cranial superstructures are in fact highly integrated, then they would not constitute separate lines of evidence in favor of restricting *H. erectus* to just the Asian part of the hypodigm.

While the focus is typically on discrete characters, differences in cranial shape have also been described, including a more angled occipital, shorter upper scale of the occipital, wider interorbital breadth, and shorter, wider face in the Asian specimens. The Asian fossils also have a higher ratio of posterior to anterior vault breadth (Antón 2003) and narrower and anteroposteriorly longer temporomandibular fossae (Bräuer 1994). In contrast, the East African sample has the greatest degree of postorbital constriction and a shorter parietal sagittal chord and arc (Andrews 1984; Stringer 1984; Wood 1984, 1991; Bräuer 1994; Bilsborough 2000). The Zhoukoudian population is characterized by a narrower biasterionic breadth and a wider biauricular breadth (Weidenreich 1943; Bilsborough 2000; Antón 2002; Kidder and Durband 2004b; Baab 2010). Yet, the scale of metric differences among temporo-geographic groups is relatively minor and broadly comparable among groups (Bilsborough 2000).

Geometric morphometric analysis of cranial vault variation within *H. erectus* found consistent differences between the African/Georgian and Asian samples but also indicated that the Zhoukoudian and Indonesian samples were at least as distinct from one another as either was from the African/Georgian fossils (Baab 2008b and Fig. 4). A more focused study of intra-Asian cranial shape variation also supported a basic Zhoukoudian–Indonesian dichotomy (although Sangiran 2 sometimes overlapped the Chinese distribution) while also identifying two main clusters within the former grouping: those from the Sangiran Dome and those from Ngandong, Sambungmacan, and Ngawi (Baab 2010), possibly reflecting phyletic change if the Sambungmacan and Ngawi fossils are as young as the Ngandong fossils.

It is possible to detect anagenetic changes in addition to regional differentiation as there is some chronological overlap among sites. Perhaps the most notable temporal trend is that of increasing endocranial volume through time (Fig. 5),

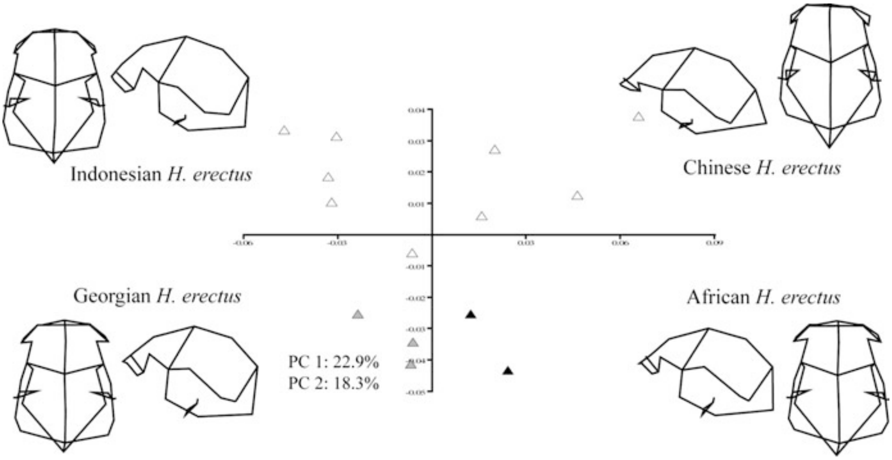

Fig. 4 Intraspecific variation in *Homo erectus* neurocranial shape. An intraspecific analysis of neurocranial shape variation in *Homo erectus s.l.* using principal components analysis of 3D cranial landmarks. This analysis uses the same landmark set as Fig. 3. There is clear geographic and temporal partitioning of cranial shape variation (wireframes represent the centroids for each geographic grouping). The first component separates the Indonesian and Chinese samples and the Georgian from African samples. The second component separates the Afro-Georgian and Asian samples. Shape differences include the narrower frontal bone and more posteriorly projecting inion of the Chinese fossils and the greater postorbital constriction of the older African and Georgian fossils. The lowest-scoring Indonesian fossil on PC 2 is also the oldest Indonesian fossil in the analysis (Sangiran 17). Legend is the same as in Fig. 2

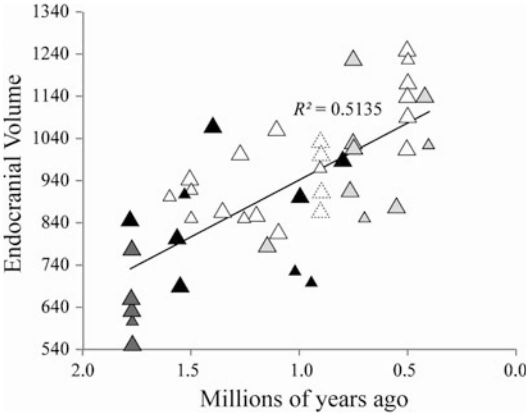

Fig. 5 Change in brain size over geological time in *Homo erectus s.l.* Bivariate plot of endocranial volume (EV) against geochronological age in a broadly defined sample of *Homo erectus*. The result indicates an increase in EV through time, but with considerable variation any given time slice. Legend is the same as in Fig. 2; the least secure estimates of EV from incomplete specimens or adult estimates based on juvenile/subadult specimens are indicated by smaller symbols, while the estimates for Sambungmacan and Ngawi have a dashed outline due to uncertainties in their provenance and therefore dating. The R^2 value shown on the plot is for the entire sample

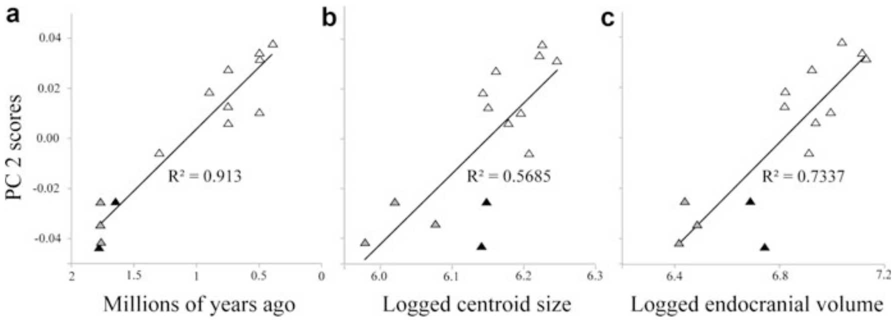

Fig. 6 The relationship between neurocranial shape and time, neurocranial size, and brain size. Bivariate plots relating principal component 2 scores (from Fig. 4) to (**a**) geochronological age of the fossils, (**b**) overall neurocranial size (natural logarithm of centroid size), and (**c**) natural logarithm of endocranial volume. Taken together, it is clear that there is phyletic change in neurocranial shape through time in *Homo erectus*, which is related in part to increasing brain size. The decrease in constriction behind the orbits observed on PC 2 makes intuitive sense when viewed in this light. Differences between endocranial volume and overall neurocranial size relate to differential cranial bone thickness and expression of ectocranial morphology, including cranial superstructures

a pattern that also holds within some regions, but not others (e.g., compare the distribution of Indonesian and African specimens on Fig. 5). Endocranial volume ranges from 646 to 1,251 cm^3. This pattern has been documented by previous workers (Leigh 1992; Rightmire 2004; Lee and Wolpoff 2009) and is confirmed here using a more complete set of *H. erectus* fossils and revised dates ($R^2 = 0.5135$). The results remain significant (and the R^2 value increases to 0.6014) when several questionable estimates from incomplete fossils (Sangiran 3, 4, and 38, Bukuran, Grogol Wetan, Ng 11, Hexian, Zkd 6, OH 12, KNM-OL 45500) and adult estimates for two juveniles (D2700, KNM-WT 15000) are excluded. As presented, the Sambungmacan and Ngawi fossils were assigned a (somewhat arbitrary) date of 0.9 Ma, but excluding them from the analysis has a negligible effect on the result ($R^2 = 0.5193$). Assigning them a younger age equivalent to Ngandong (0.5 Ma) reduces the R^2 value slightly to 0.4760. Excluding the 12 fossils with the most problematic EV estimates in addition to the Sambungmacan and Ngawi specimens strengthens the association ($R^2 = 0.6156$).

Cranial shape also varies as a function of time, although many fewer specimens can be examined (Baab 2007). For example, the position of fossils along the second principal component shown in Fig. 4 is strongly correlated with geological age (Fig. 6a). While some of this shape change is attributable to the underlying increase in cranial capacity, the fit between geological age and PC 2 scores is better than between cranial size and PC 2 scores (Fig. 6b) or between endocranial volume and PC 2 scores (Fig. 6c). Additional temporal trends have been documented by Kaifu and colleagues within Sangiran and across Indonesia more broadly (Kaifu et al. 2005, 2008).

Implications of Newly Described Fossils for *Homo erectus* Systematics

Since the 1980s, a number of fossils were recovered from China, Indonesia, Africa, and Georgia that compare favorably with other *H. erectus*. Some of these have been evaluated in a comparative context and appear to fall within the boundaries established previously for the species, including the Chinese Nanjing I cranium (Liu et al. 2005) and the Indonesian fossils Skull IX (Tjg-1993.5) (Arif 2005; Kaifu et al. 2011), Bukuran (Grimaud-Hervé et al. 2005; Grimaud-Hervé et al. 2012), Grogol Wetan (Widianto and Grimaud-Herve 2000), Sambungmacan 4 (Baba et al. 2003a), and Bpg 2001.04 (Zaim et al. 2011).

Other recently described fossils attributed to *H. erectus* differ in some way from the average configuration. The two Yunxian crania from China resemble other *H. erectus* in their overall low and elongated cranial vaults, but exhibit more derived facial features, in common with *H. antecessor* or *H. sapiens* (Li and Etler 1992; Etler 1996, 2004; Vialet et al. 2010), although Zhang (1998) raised concerns about the accuracy of character evaluations due to deformation of the fossils. Sambungmacan 3, while sharing many detailed anatomical resemblances to other Sambungmacan and Ngandong fossils, lacks an angular torus (Márquez et al. 2001), and geometric morphometric analysis indicates that its rounded frontal bone and less sharply angled occipital create a midsagittal profile that is intermediate between fossil *Homo* and *H. sapiens* (Delson et al. 2001). Sambungmacan 3 is more closely affiliated with *H. erectus* than modern humans based on its overall vault shape (rather than just the midsagittal profile), but its globular neurocranium positions it at the periphery of the *H. erectus* distribution, closer to more derived *Homo* (labeled in Fig. 3). The overall pattern of metric and nonmetric similarity between Sambungmacan 3 and other Indonesian *H. erectus* supports its inclusion in the species. Some fossils that have been known for a longer time also remain enigmatic, such as SK 847 from Swartkrans (e.g., Grine et al. 1996).

Among the most noteworthy potential additions to the *H. erectus s.l.* hypodigm since the 1980s are the fossils from Dmanisi. Descriptions of four crania and four mandibles, as well as numerous postcranial bones, were published between 1992 and 2007 (Gabunia 1992; Gabunia and Vekua 1995; Gabunia et al. 1999, 2000; Vekua et al. 2002; Lordkipanidze et al. 2005, 2007). Their cranial vault profiles are typical of *H. erectus* in being long and low with prominent supraorbital tori. Some individuals also exhibit midline keeling, occipital tori, and other discrete traits common to *H. erectus*. However, the cranial capacities of these individuals are smaller than any of the Asian fossils and the KNM-ER 3733 and 3883 and OH 9 fossils from Africa. A description of the fifth cranium (D4500) from this site was published in 2013 and diverges from the other four in having an even smaller endocranial volume (546 cm^3) but a large and prognathic face. It also exhibits the most well-developed cranial superstructures of any of the Georgian fossils, including a large supraorbital torus, occipital torus, and supramastoid crests, although midline keeling is restricted to the posterior sagittal suture and a “lambdoid hump” creates a more vertical occipital squama that is typical in

H. erectus (Lordkipanidze et al. 2013). This individual, as well as D3444, may well represent males while the others were females, possibly providing the best glimpse currently available into sexual variation in this species.

Although extensive, the degree of cranial shape variation (particularly in terms of facial rather than neurocranial morphology) within the Dmanisi sample is comparable to populations of chimpanzee species as well as humans. The authors interpret this variation as indicative of higher levels of intraspecific variation than normally recognized for fossil hominins (at least partially due to sexual dimorphism) and use this observation to argue for a single, geographically widespread *H. erectus* species ranging from East and South African north to Georgia and east to China and Indonesia (Lordkipanidze et al. 2013). Yet, the description also emphasizes morphological affinities between the new Georgian cranium and African fossils attributed to *H. habilis*/*rudolfensis*, and the authors hint at subsuming these taxa within *H. erectus s.l.* (but see Spoor et al. 2008; (chapter "▶ Defining Hominidae," Vol. 3). Other Dmanisi fossils also exhibit aspects of facial form and dentition that are more primitive than KNM-ER 3733 and 3883 (Vekua et al. 2002; Martinón-Torres et al. 2008; Rightmire and Lordkipanidze 2009). Given their antiquity, this pattern could be reconciled by positing an early migration of this population soon after the origin of the species (or even a Eurasian origin for *H. erectus s.l.*) and does not require the recognition of a distinct species. Yet, it must also be acknowledged that this "solution" does blur the morphological boundaries between *H. habilis*, *H. rudolfensis*, and early *H. erectus* (Rightmire and Lordkipanidze 2009; Lordkipanidze et al. 2013), a similar concern noted by Wood (1984) in reference to the inclusion of KNM-ER 3733 and 3883 in *H. erectus*.

One European fossil was recently assigned to *H. erectus* from Kocabaş, Turkey, and dated to the Middle or possibly Lower Pleistocene. This fossil is quite incomplete, but both the initial description (Kappelman et al. 2008) and a subsequent linear morphometric comparative analysis of the reconstructed specimen (Vialet et al. 2012) emphasized its affinities with *H. erectus* fossils. The comparative analysis was not complete, however. For example, it did not include any of the Ngandong specimens which may be of similar Middle Pleistocene age, but which are likely to be much larger in overall size, or the small *H. heidelbergensis s.l.* fossil from Ceprano, Italy. The Kocabaş fossil also lacks a midline keel on the parietal bones. Therefore, while this fossil may represent a second Eurasian *H. erectus* site, its incomplete nature and the limited comparative analyses leave open other possibilities.

Two fossils described from Kenya in the 2000s are separated geologically by ~0.6 Myr but share an important feature – both are quite small. KNM-ER 42700, with an estimated cranial capacity of 691 cm^3 (Spoor et al. 2007), is smaller than other similarly aged fossils, but within the range of the Georgian fossils. This calvarium exhibits some discrete traits typical of *H. erectus*, such as keeling on the frontal and parietals and a supratoral sulcus, but not others, including thick cranial vault bones, a prominent supraorbital torus, and an occipital torus (Spoor et al. 2007), and its cranial shape is outside of the bounds of *H. erectus*, including the Dmanisi fossils (Baab 2008a). The interpretation of these results is complicated somewhat by the older subadult or young adult status of this fossil, but a subadult from Dmanisi, D2700, is much more similar to other *H. erectus*. KNM-ER 42700 also suffered some postdepositional deformation, primarily affecting the position of the frontal bone (Spoor et al. 2008). Reanalysis without frontal bone landmarks yields the same result as the original analysis (i.e., KNM-ER 42700 is quite distinct in its posterior cranial vault shape from *H. erectus*; unpublished data). KNM-OL 45500 from Olorgesailie is a more fragmentary specimen but is clearly a small individual (Potts et al. 2004). Its frontal bone shape is most similar to other *H. erectus*, falling outside of the previously documented range of variation, but not in the direction of any other *Homo* species (Baab 2007). The shape analysis may be affected by preservation issues, but its basic patterns of a distinct supraorbital torus with a continuous supraorbital sulcus and marked postorbital constriction are all consistent with attribution to *H. erectus*. Its inclusion does, however, increase both size and shape variation during this time period (0.9 Ma) and possibly for the species as a whole since it exhibits very small dimensions of the frontal and temporal bones.

Two other African crania have been described from a similar time period, one of which was explicitly attributed to *H. erectus* (the Daka calvarium from Ethiopia, 1 Ma) and one of which was compared favorably to *H. erectus*, although the authors fell short of actually assigning it to this species (the Buia cranium from Eritrea, 0.8 Ma). These specimens are of average size for this time period, but much of their morphology is clearly derived relative to other *H. erectus*, particularly the more vertical cranial vault sides and higher, more rounded vaults. Both fossils also have very tall supraorbital tori, a feature common to *H. heidelbergensis s.l.* Neither fossil has a well-developed occipital torus or an angled occipital bone. Yet the two fossils are not identical – the Buia fossil is much narrower for its length and height than the Daka fossil, and there is a marked glabellar depression in the Daka fossil absent in the Buia fossil. Two reasonable explanations for the derived morphology seen in the Daka and Buia fossils are that each may represent either an "advanced" *H. erectus* on the lineage leading to later *Homo* or an early member of a more derived *Homo* species. Thus, the Daka and Buia fossils present a situation similar to the Dmanisi fossils in that their inclusion in *H. erectus* serves to blur the distinction between *H. erectus* and later *Homo* taxa. However, if the Dmanisi fossils are included in *H. erectus* due to the presence of derived *H. erectus* characters, then, by the same logic, the Daka and Buia fossils should be assigned to a later taxon based on the presence of traits derived with respect to the rest of the *H. erectus* hypodigm.

Discussion

Clearly much of the variation in cranial shape and discrete cranial features is structured along geographic and temporal lines. This raises the question of whether differences among geographically and possibly temporally restricted samples should be read as support for a single, polytypic species or for multiple species.

In support of the former, members of *H. erectus s.l.* are united by a remarkably consistent cranial *Bauplan* with more minor geographic and temporal variations superimposed on this basic form (e.g., Rightmire 1990; Antón 2003). Furthermore, variation between African/Georgian and Asian fossils is comparable to that seen within the Asian sample. A variety of factors can contribute to interpopulation variation, including adaptation to local environments, genetic drift (Antón 2002, 2003), species-wide temporal trends (e.g., increasing brain size; Rightmire 2004; Lee and Wolpoff 2009), and in situ evolutionary change (Kaifu et al. 2008, 2011). In support of a multiple-species model, a few studies have found morphological variation to be in excess of single primate species (Villmoare 2005; Skinner et al. 2006) and, more importantly, autapomorphic features are more heavily concentrated in the Asian fossil record (e.g., Wood 1984).

Paleontological species are defined based on morphological characters that are themselves implicitly believed to signal the boundaries of a gene pool. Given that species are descended from preexisting species and that some will also give rise through speciation events to additional species, the characters that form the basis of this definition will in many cases be a combination of both plesiomorphic and synapomorphic traits. Species with no descendants may also be delineated by autapomorphic characters. However, speciation events rarely entail the entirety of a species but rather a subsample of that species (i.e., allopatric speciation). It is therefore conceivable that a species which gave rise to one or more daughter species could still have contained populations that exhibit autapomorphies. Therefore, although the arguments are finely balanced, the evidence from morphology is insufficient to overturn the null hypothesis of a single species for the core *H. erectus* hypodigm (those found in Africa and Asia through the 1980s). The position of more recently described fossils from Asia, but more importantly from Africa, needs to be assessed relative to these established patterns to evaluate whether these fossils expand the morphological range of *H. erectus*, and if so, whether this expansion is consistent with expectations for a single species. In other words, accepting a polytypic species model for *H. erectus* does not imply that this species must or should become a “wastebin” taxon.

The location of the oldest fossils attributed to *H. erectus* in East Africa is most consistent with an origin of *H. erectus* in East Africa, likely from an ancestor similar to *H. habilis*. However, this hinges on the correct identification and dating of KNM-ER 2598 as *H. erectus* at 1.9 Ma in the Turkana Basin (Wood 1991). Otherwise, *H. erectus* appears more or less simultaneously in East Africa and Eurasia, and the possibility of a Eurasian origin of *H. erectus* has been raised (White 1995; Asfaw et al. 2002; Dennell and Roebroeks 2005). On the one hand, the presence of a potential ancestral species, *H. habilis*, in East Africa is further support for an African origin. On the other hand, the presence of *H. floresiensis* in Indonesia with its *H. erectus*-like cranial morphology but unexpectedly primitive postcranial and dentognathic morphology (Brown and Maeda 2009; Jungers 2009; Jungers et al. 2009; Baab et al. 2013) may imply the presence of a more ancient dispersal through mainland Asia. In either case, origin was followed by rapid dispersal (to either Eurasia or East Africa, depending on the location of the origin).

What happened subsequent to this migration is less clear. Kaifu and colleagues suggest a similarly early migration to Java on the basis of primitive dentognathic fossils in the early Sangiran hominin fossil record (Kaifu et al. 2005). Certainly, there was at least one, but possibly more than one, migration to East Asia and possible back migration from Asia to Africa (Dennell and Roebroeks 2005; Zaim et al. 2011), and the degree of gene flow among populations remains obscure. Populations in China and Indonesia survived into the Middle Pleistocene, and, at least in Indonesia, there is evidence of additional in situ evolutionary change from the Lower to Middle Pleistocene (Kaifu et al. 2008). Most researchers view the Asian populations as evolutionary dead ends, although some see links between Chinese *H. erectus* and *H. antecessor* (Carbonell et al. 2005). In contrast, many workers see portions of the African *H. erectus* fossil sample as potential ancestors to later species, such as *H. antecessor* (Bermúdez de Castro et al. 1997, 1999) or *H. heidelbergensis s.l.* (Andrews 1984; Rightmire 1990, 2008; Wood 1994; Asfaw et al. 2002).

Not surprisingly, both early and late members of the species present a challenge because they may resemble more primitive or derived species, respectively. At the early end of the time range, the Dmanisi fossils further blur the distinction between *H. habilis*, *H. rudolfensis*, and *H. erectus*, while at the more recent end, Daka and Buia exhibit cranial traits that overlap *H. heidelbergensis s.l.* The latter case is particularly interesting as it signals a divergence between the African and Asian fossils in regard to cranial evolution in response to increased brain size since more recent (and larger-brained) fossils from Indonesia (e.g., Ngandong) do not converge on the *H. heidelbergensis* morphotype as strongly. This creates a situation familiar from the European Middle Pleistocene: Daka and Buia could be interpreted as "pre-*H. heidelbergensis s.l.*" or "pre-*H. rhodesiensis*," much as the Sima de los Huesos (and some other European fossils) are characterized as pre-Neanderthals. The controversy over how to treat a chronospecies from a taxonomic perspective would then also apply here (e.g., Bermúdez de Castro et al. 1997; Hublin 2001; Stringer 2012).

More generally, the increase in the size of the fossil sample has created a new set of challenges for *H. erectus* systematics. As Antón (2003, p. 162) argued:

> . . .the greater the fossil data set, the less clear the boundaries between taxa appear to be, and the more critical it becomes that we understand the structure, function, and development of the characters that appear to separate or unite our fossil groups. Understanding the function, developmental origins, and underlying variability of these features in extinct and extant primates remains an imperative task.

The expression of discrete traits across geographic regions and through time needs to be systematically reevaluated given the expansion of the fossil hypodigm assigned to *H. erectus*. The accessibility of technologies such as laser surface scanning and computed tomography also opens the door to better options for quantifying discrete traits that have traditionally been assessed visually and described qualitatively. Furthermore, a fruitful direction for future research is the clarification of the etiology of discrete traits used to define and differentiate among

Pliocene–Pleistocene *Homo* taxa. Do these traits have a genetic basis? Are they adaptive or do they retain a primarily stochastic signal? Are these traits independent or is their expression integrated with other aspects of morphology? A diverse range of tools can be used to address these questions, including quantitative genetics, animal models, correlative approaches using modern humans, and analysis of integration.

Conclusion

This review highlights that one of the most consistent features tying together different fossils assigned to *H. erectus s.l.* is cranial vault shape which is generally low and elongated with greatest width across the supramastoid or mastoid crests, a sloping frontal bone with marked postorbital constriction, and an angled occipital bone. While less commonly preserved, the facial skeleton may be more variable. Cranial superstructures, along with a handful of other discrete traits of the cranial vault, also serve to unite many of the fossils but are less consistently expressed across individuals. While the overall frequency may be higher in the Asian fossils, they do not serve to clearly distinguish among subsets of the larger hypodigm. Phyletic change in *H. erectus* through time is due in part to an increase in brain size, but both geographic and temporal variations also likely reflect microevolution and local adaptation.

Morphological evidence supports the interpretation of *H. erectus* as a polytypic species comprising fossils primarily from Lower to Middle Pleistocene sites in China, Indonesia, East Africa, Eurasia, and possibly South Africa. Current evidence suggests that the origins of this species lie in Eurasia or East Africa, and this species likely contains the population ancestral to more derived *Homo* species, such as *H. antecessor* or *H. heidelbergensis*. Yet, the recognition of a geographically and temporally widespread species should not encourage incautious attribution of fossils to this species, lest we create another “wastebin” species. Proposed additions that do not fit the established morphological bounds of the species should be evaluated in terms of how much they extend the magnitude of variation relative to extant analogs and whether they extend the range in a way which is consistent with intraspecific patterns of variation documented for this species. Geometric morphometric analysis of cranial shape has helped to clarify how the cranial shape of *H. erectus* fits into a broader *Homo* context, as well as identifying differences among spatiotemporal groups (perhaps equivalent to paleodemes). Additional work quantifying discrete traits, establishing their distribution in the expanded Pleistocene *Homo* fossil record, and establishing the utility of these traits in systematic applications will further clarify the boundaries of *H. erectus* as a species.

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Cross-References

- ▶ Defining the Genus *Homo*
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Later Middle Pleistocene *Homo*
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Modern Humans
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Earliest Putative *Homo* Fossils
- ▶ Virtual Anthropology and Biomechanics

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Later Middle Pleistocene *Homo*

G. Philip Rightmire

Contents

Abstract

Hominin fossils are known from Middle Pleistocene localities in Africa, Europe, South Asia, and the Far East. It is recognized that these individuals display traits that are derived in comparison to the condition in *H. erectus*. However, the skulls retain numerous primitive features that set them apart from modern humans.

G.P. Rightmire (✉)
Department of Human Evolutionary Biology, Harvard University, Peabody Museum, Cambridge, MA, USA
e-mail: gprightm@fas.harvard.edu

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Faces are massively built with strong supraorbital tori, frontals are flattened, and vaults remain low with less parietal expansion than in *Homo sapiens*. The hominins from Bodo, Broken Hill, and Elandsfontein in Africa are quite similar to their Middle Pleistocene contemporaries in Europe. Crania and jaws from Arago Cave and Petralona, and the spectacular assemblage from Sima de los Huesos, are particularly informative. In sum, this evidence suggests a speciation event in which *H. erectus* gave rise to a daughter lineage. At or before the beginning of the Middle Pleistocene, new populations spread through Africa and western Eurasia and perhaps also to the Far East. How the fossils should be treated taxonomically is currently uncertain. One view emphasizes gradual anagenetic change, while others advocate speciation occurring repeatedly throughout the Pleistocene. In the perspective favored here, differences between the Middle Pleistocene hominins can be attributed to geography, time, or intragroup variation. Many, if not all, of the European and African specimens can be accommodated in one species distinct from Neanderthals and modern humans. If the Mauer mandible is included in this hypodigm, then the appropriate name is *H. heidelbergensis*. This species is probably ancestral to both the Neanderthals in Europe and the earliest representatives of *H. sapiens* in Africa.

Introduction

Humans evolved in Africa and were confined to that continent for much of their early history. The first dispersals from Africa into Eurasia occurred near 2 million years ago (Ma). These migrants were probably representatives of *Homo erectus* (sometimes called *Homo ergaster*). Traces left by these hominins have been recovered from the site of ‘Ubeidiya in the central Jordan Valley and at Dmanisi in the Georgian Caucasus. Some early occupations were likely transitory and did not result in permanent settlements. However, groups of *H. erectus* were able to travel relatively quickly across southern Asia to the Far East, where they were established both in Java and in China by 1.7–1.6 Ma. The first penetration westward into Europe apparently came much later. There are indications that humans were moving into the Mediterranean region prior to 1 Ma, but the initial populating of Europe north of the major mountain barriers is documented only after about 700 thousand years ago (Ka). The biological identity of the first Europeans is unclear, but it is agreed that these hominins differ from *H. erectus*. Many of the ancient fossils are presently assigned to the species *H. heidelbergensis* (named originally from a mandible found near Heidelberg in Germany). *Homo heidelbergensis* or perhaps other closely related species are known also from Middle Pleistocene localities in Asia and Africa (Fig. 1). These people seem to have been more advanced in behavior than their predecessors, and there is evidence that *H. heidelbergensis* was able to make relatively sophisticated stone tools, hunt larger and more dangerous game animals, and perhaps engage in cooperative social activities.

Fig. 1 Map giving the locations of Middle Pleistocene localities where important hominin fossils have been discovered

The Middle Pleistocene of Africa

In Africa, fossils from the early Middle Pleistocene are clearly different from *H. erectus* in cranial capacity (approximately equal to brain size), width of the frontal bone, proportions of the occipital region, and anatomy of the underside of the skull. Where it is preserved, the face is still heavily constructed, but the brows, nasal profile, and bony palate more closely resemble the condition seen in later humans. In many instances, the hominins are found with stone tools that are more carefully shaped than the choppers and relatively crude hand axes associated with *H. erectus*. From Bodo in Ethiopia to Elandsfontein in South Africa, a shift toward the manufacture of thinner, more finely flaked bifacial tools is documented in the Middle Pleistocene, and it is reasonable to link this change in behavior to a speciation event in which *H. erectus* gave rise to a daughter lineage exhibiting increased relative brain size (encephalization).

Bodo

One important specimen came to light in 1976 at Bodo, in the Middle Awash region of Ethiopia (Fig. 1). The Bodo cranium and later a broken parietal from a second

Fig. 2 Facial and oblique views of the cranium from Bodo, Ethiopia. The projecting glabellar region, wide interorbital pillar, and massive zygomatic (cheek) bones give the face an archaic appearance similar to that of *H. erectus*. Other traits including the vertical border of the nasal aperture are interpreted as apomorphies shared with later humans

individual were found in conglomerates and sands containing mammalian bones and Acheulean tools (Kalb et al. 1980; Clark and Schick 2000; Gilbert et al. 2000). Fauna from the Bodo site has been compared to that from Bed IV at Olduvai Gorge and Olorgesailie in Kenya, and an early Middle Pleistocene date is indicated. ^{40}Ar/^{39}Ar measurements reported by Clark et al. (1994) support this biochronology, and the evidence points to an age of about 600 Ka for the Bodo hominins.

The face and the anterior part of the Bodo braincase are preserved (Fig. 2). There are some cut marks on the facial bones, and these indicate intentional postmortem defleshing, as documented by White (1986). It can be established that Bodo is like *H. erectus* in some features. The massive facial bones, projecting brow, low frontal with midline keeling, parietal angular torus, and thick vault give the specimen a pronounced archaic appearance. In other respects, the cranium is more specialized (derived) in its morphology. Brain size is close to 1,250 cm^3 and is thus substantially greater than expected for *H. erectus*. Frontal bone proportions, the high-arched shape of the squamous temporal, and some traits of the cranial base are like those of more modern humans. Although the face is very broad and heavily constructed, the supraorbital tori are divided into medial and lateral segments, the margin of the nose is vertical rather than forward sloping, and the incisive canal opens into the front of the hard palate (Rightmire 1996). These are derived (apomorphic) conditions present in the face of recent *Homo*.

Broken Hill and Elandsfontein

Another African specimen is the cranium from Broken Hill (now Kabwe) in Zambia, discovered by miners in 1921. Quarrying for lead and zinc ore had already removed most of a small hill, when the miners broke into the lower part of an extensive cavern. Published reports do not all agree on this point, but apparently the cranium was picked up by itself, not in clear association with other hominin remains. The fossil is in remarkably good condition. The face is massive, with some of the heaviest brows on record. The frontal is flattened with slight midline keeling, and the vault is low in profile. Shortly after it was found, the fossil was attributed to the (new) species *H. rhodesiensis* (Woodward 1921). In its overall morphology, however, Broken Hill resembles *H. erectus*, and indeed, it has been classified this way on more than one occasion. At the same time, there are apomorphic features shared with later humans. The temporal squama is high and arch shaped, and the upper scale of the occipital is expanded relative to its lower nuchal portion (where the neck muscles are attached). Several discrete characters of the temporomandibular joint region are specialized. These include a raised articular tubercle and a sphenoid spine. More changes are apparent in the face, where the lateral border of the nasal aperture is set vertically, and the palatal anatomy is like that of later people (Rightmire 2001).

Another cranium quite similar to that from Broken Hill comes from the farm Elandsfontein, near Saldanha Bay on the Atlantic coast of South Africa. At Elandsfontein, there is an expanse of sandveld that has long been a focus of attention for paleontologists. Dunes migrate across this area, and in between the dunes, there are swales resulting from deflation. Whether the ancient horizons exposed in these “bays” are stratified land surfaces or simply mark the (seasonal) fluctuations of the water table is unclear. Given either of these interpretations, it is evident that during the mid-Quaternary, the region supported wetlands and water holes, with plenty of grass (Deacon 1998). Animals, many of them bovids or other large herbivores, were attracted to the water. The fauna includes numerous archaic elements such as a dirk-toothed cat, a sivathere, and a giant buffalo. Altogether, some 15 of 48 mammalian species collected at the site have no historic descendants. Comparisons conducted by Klein and Cruz-Uribe (1991) imply that the bones were accumulated between 700 and 400 Ka, but more recent sorting of the fauna suggests an older interval, between 1 Ma and 600 Ka (Klein et al. 2006).

Much of the work at Elandsfontein has been surface prospecting, and it was during one such visit in 1953 that investigators picked up pieces of a human skullcap. The reconstructed Elandsfontein cranium is composed of the frontal and parietal walls and some of the occiput. The bones are cracked and heavily weathered, but the braincase is not distorted. There are some similarities to *H. erectus*, but certainly the better match is with Broken Hill. These two Middle Pleistocene specimens are alike not only in overall proportions but also in many anatomical details. The Elandsfontein brow is almost as thick as that of Broken Hill, and the frontal contours are the same. Radiographs show that the frontal sinus is large and complex, reaching well up into the squama in both cases (Seidler et al. 1997; Rightmire unpublished observations). The South African frontal bone gives a breadth index of 91.9 and is thus slightly less constricted than that of Broken Hill, for which the ratio of least width to greatest breadth is 83.0. Sagittal and coronal measurements of the parietal are similar in the two individuals as is the length and orientation of the upper scale of the occipital. Unfortunately, the Elandsfontein base is missing, and there is no face. These are just the regions where one would expect to find additional apomorphies setting the South African hominin apart from *H. erectus*.

Lake Ndutu

A fourth Middle Pleistocene specimen is known from Lake Ndutu. This seasonal soda lake is located at the western end of the Main Gorge at Olduvai, in northern Tanzania. Excavations conducted near the lake margin in 1973 produced an encrusted human cranium, along with other fossils and numerous artifacts (Mturi 1976). Initially, the stone assemblage included mostly spheroids, cores, and flakes, but hand axes were picked up during later visits to the site. All of this material is thought to be derived from archaeological horizons in a greenish sandy clay, tentatively correlated with the upper Masek Beds at Olduvai.

When it was found, the cranium was severely damaged and encased in a clay matrix. The process of cleaning and reconstructing the fossil has been described by Clarke (1990). These efforts were generally successful, but the face is quite incomplete, as is the frontal bone. There are gaps in the parietals as well. The braincase is relatively small, with a capacity of only about 1,100 cm^3. Just a fragment of the supraorbital region is preserved, and the torus is projecting, if not especially thickened. Bossing of the parietals is emphasized in Clarke's reconstruction. This has perhaps been overdone with plaster, but the walls of the vault appear to be more convex than would be the case for *H. erectus*. Also, the upper plane of the occiput is vertical, above the moundlike transverse torus. The morphology of this torus is in keeping with other characters suggesting that Ndutu could be female, in comparison to males such as Bodo or Broken Hill.

Florisbad

Several additional fossils are more fragmentary and therefore somewhat less informative. An example is the cranium from spring deposits at Florisbad in South Africa, consisting only of facial parts, the frontal bone, and pieces of the parietals. Early studies compared the hominin to recent populations, but it is important to emphasize that Florisbad is far from modern in its morphology. Glabella (in the midline above the nasal root) is projecting, as is the brow on either side. The facial bones as repositioned by Clarke (1985) suggest that the nasal cavity is large and the cheek is flattened, without obvious infraorbital hollowing. The face is less heavily constructed than that of Broken Hill but otherwise not dissimilar. A human upper molar tooth from Florisbad has been dated by ESR to 259 Ka (Grün et al. 1996).

The Omo Localities and Herto

Several sites in the Omo region of southern Ethiopia, explored initially in 1967, have recently been revisited. Human remains are known from Member I of the Kibish Formation, now considered to be 200–100 Ka in age (Assefa et al. 2000). Omo 2 is an isolated surface find from PHS, lacking archaeological associations. This partial cranium is low in contour and decidedly massive in its construction, with a blunt frontal keel and a strongly angled occiput. Other likely primitive features include the shape of the deep mandibular cavity lacking any distinct articular tubercle and the absence of a sphenoid spine. Nevertheless, the vault is large overall. The frontal bone is broad and relatively unconstricted, and the parietal walls show some outward curvature (limited to the regions below the temporal lines). The supraorbital torus is extensively damaged, and none of the face is preserved.

Omo 1 was excavated at the KHS site, dated to 195 Ka (McDougall et al. 2005), from which there is now a large collection of Middle Stone Age artifacts. This individual is represented by only small portions of a skull, but much more of the postcranial skeleton is present. The cranium as reconstructed by several workers is globular in form, with expanded parietals and an occipital that is more rounded than that of Omo 2. To the limited extent that these can be checked, cranial superstructures (crests and tori) are not strongly expressed. The anterior part of the mandible shows clear signs of chin formation. Given these important markers of modern morphology, there is general agreement that Omo 1 should be regarded as early *H. sapiens*.

An important question, still not firmly resolved, is whether the Omo 1 skeleton can be grouped with the more archaic Omo 2 remains or whether these individuals should be placed in separate populations. The morphological differences between the two crania are very substantial. Indeed Omo 2 has been compared to specimens such as Broken Hill or Elandsfontein, even though the frontal is rather less narrowed behind the orbits. If the Omo fossils are approximately the same age, then there are two possibilities. Omo 2 may be a remarkably robust individual, within a highly variable but essentially modern population. Alternatively, this specimen can be regarded as representative of an archaic, late-surviving lineage, present alongside anatomically modern humans. However, if Omo 2, picked up on the surface, is actually older than implied by recent dating for the PHS site, then it is easier to argue that the cranium is sampled from an earlier portion of the lineage ancestral to *H. sapiens*.

Specimens from Herto in the Middle Awash region confirm the presence of *H. sapiens* in northeastern Africa late in the Middle Pleistocene. Three fossilized crania recovered in 1997 show cut marks associated with postmortem defleshing and are associated with a stone tool assemblage that can be characterized as late Acheulean or Middle Stone Age. The bones and artifacts are dated radioisotopically to between 160 and 154 Ka (Clark et al. 2003). One of the adult crania

(BOU-VP-16/1) is intact, with a brain size estimated as 1,450 cm^3 (White et al. 2003). This individual is ruggedly built, with a very prominent, bilaterally arched glabella, a long vault, and a distinctly flexed occipital. The parietal walls are convex rather than inward sloping, and the index of neurocranial globularity (Lieberman et al. 2002) calculated as ca. 0.54 for BOU-VP-16/1 is high enough to be within the range expected for anatomically modern humans. A second adult cranium is less complete, and there is a child estimated as 6–7 years in age. As a group, the Herto individuals are very robust but display morphologies that place them close to recent populations. White et al. (2003) have referred the fossils to a new subspecies of *H. sapiens*.

Middle Pleistocene Hominins from Europe

Skulls very similar to those from Africa have been found in western Eurasia. Several of the principal localities lie close to the Mediterranean Sea, but it is apparent that humans were also able to reach Britain and central Europe, relatively early in the Middle Pleistocene (Fig. 1).

The Cranium from Petralona

Petralona lies near the city of Thessaloniki in northern Greece. The exact provenience of the hominin fossil found within cave deposits containing the bones of numerous extinct animals is uncertain, but the Middle Pleistocene antiquity of this material is not in doubt. The cranium itself is exceptionally well preserved (Fig. 3)

Fig. 3 Lateral and facial views of the cranium from Petralona, Greece. This European hominin resembles Middle Pleistocene specimens from Africa. The Petralona and Broken Hill individuals are especially similar in measurements relating to facial proportions and vault shape

and would have enclosed a brain close to 1,230 cm^3 in volume (Stringer et al. 1979). Supraorbital tori are about as massive and projecting as in Broken Hill, while CT scans show that the frontal sinuses are greatly expanded. These air cavities extend posteriorly toward bregma and also laterally, where they are separated from the sphenoid sinuses only by thin bony partitions (Seidler et al. 1997). The frontal bone itself is relatively shorter and broader than in Broken Hill. The ratio of least to greatest frontal breadths is 91.6; postorbital constriction is thus less pronounced than in Broken Hill but comparable to that estimated for the Elandsfontein specimen. Petralona also differs from Broken Hill in having a wider cranial base and a less prominent torus crossing the occipital bone. However, the two hominins are alike in many other aspects of vault shape, in orientation of the infraorbital region, and in several measures of facial projection (Rightmire 1998, 2001; Friess 2010; Harvati et al. 2010, 2011).

Arago Cave

Much the same conclusion applies to the less complete cranium from Arago Cave in France dated to about 450 Ka. The partial cranium numbered Arago 21 has a face that is largely intact but damaged as a result of its long interment in compacted cave sediments. The frontal bone, interorbital pillar, nose, and cheeks show numerous cracks, and areas of localized crushing are present. The discoverers have been able to correct some of this damage in a reconstruction, but significant distortion remains. Nevertheless, it is evident that Arago 21 is somewhat smaller than Petralona or Broken Hill in brow thickness, upper facial width, and facial length. Height of the bony orbit and the subnasal part of the maxilla are especially reduced, and the nasal saddle seems to be less elevated relative to the orbital margins. Apart from these differences, Arago 21 is similar in its proportions to the Broken Hill cranium from Africa (Rightmire 2001).

Some workers discern resemblances to Neanderthals. Hublin (1996) and Arsuaga et al. (1997) note that the infraorbital surface of the Arago 21 maxilla is flattened and the cheek bones are obliquely oriented, as in Neanderthals. Also, there is forward protrusion of the face at subspinale (in the midline, just below the nasal opening), and the nasal aperture is bounded inferiorly by a sharp rim. These observations must be tempered by the fact that cracking and plastic deformation make it difficult to assess key aspects of morphology. The wall of the Arago 21 maxilla is generally flattened or even inflated in the manner characteristic of Neanderthals, but the cheek is slightly hollowed laterally, below the orbit. This feature cannot be due entirely to damage. Also, it is not clear that the zygomatic bone is swept back (obliquely oriented) so noticeably as in later European populations. In facial forwardness at subspinale [as measured by the zygomaxillary angle of Howells (1973)], Arago 21 at 113° is in the Neanderthal range, and Petralona at 118° shows almost as much protrusion. But the value for Broken Hill is only 116°, so a low zygomaxillary angle does not align Arago 21 and Petralona with Neanderthals rather than with other Middle Pleistocene specimens. The sharp inferior margin of the Arago nose is indeed reminiscent of that in Neanderthals. However, there is variation in this feature. Petralona is rather less like the Neanderthals, while some later Europeans including the Sima hominins (section "Sima de los Huesos, Atapuerca") have a pattern of cresting on the nasal floor resembling that in Broken Hill or Bodo.

In addition to the partial cranium, the cave at Arago has yielded several mandibles, of which two have been described. Arago 2 is the more complete, missing only the angle and ascending portion from the left side. This specimen has sustained damage anteriorly, where the symphysis and left corpus are cracked. Arago 13 is a large hemimandible (right side), in relatively good condition. Both specimens present a mix of archaic and more modern characters. Development of the lateral prominences, marginal tori and tubercles, and internal symphyseal buttresses is comparable to that observed in *H. erectus*, although the alveolar planum is steeper and less shelflike in the Arago individuals. Arago 2 displays definite incurving of the symphyseal face below the alveolar border. Here, the elements of a mental trigone are present, while in Arago 13, signs of "chin" formation are less clear. Both jaws have retromolar fossae. However, in Arago 13, this fossa is restricted, and the crown of M_3 is partly obscured by the leading edge of the ramus when the specimen is viewed from the side.

The Arago mandibles are important not only because they reveal information about a Middle Pleistocene hominin population but also because they can be compared to the jaw from Mauer, near Heidelberg in Germany. Assigned a radiometric age of 609 Ka (Wagner et al. 2010), the Mauer fossil is likely to be one of the oldest recovered in Europe. It has often been described as primitive, with a massive body and very thick symphysis lacking any mental eminence. At the same time, the broad ramus, increased symphyseal height, and moderate size of the teeth suggest a morphological pattern different from that of *H. erectus*. The mandible was referred to the (new) species *H. heidelbergensis* by Schoetensack (1908). As the Arago jaws resemble the Mauer specimen, it is possible to link the French assemblage with the same taxon. Similarities of the Arago 21 face to Petralona (or Broken Hill) in turn provide a formal basis for including other European (or African) individuals in *H. heidelbergensis*.

Sima de los Huesos, Atapuerca

The species *H. heidelbergensis* is increasingly well documented by the spectacular finds from Atapuerca in northern Spain. Excavations in the Sima de los Huesos have produced hominin remains, representing virtually all parts of the skeleton, that their describers have attributed to *H. heidelbergensis*. In addition to skulls, there are many postcranial bones, and it is clear that at least some of the Sima (male) individuals were tall and robust (Arsuaga et al. 1999a). Somewhat surprisingly, sexual dimorphism is comparable to that expressed in recent populations. The cave also contains the bones of bears and a few other carnivores, but there are no herbivores that might represent food waste. With one exception, there are no stone artifacts. A single hand axe fashioned from red quartzite was discovered in 1998. Investigators working at the Sima have argued that the skeletons were deposited in this pit by other humans and that the unique hand axe documents symbolic behavior (Carbonell and Mosquera 2006). First application of U-series dating to a speleothem present in the lower part of the stratigraphic sequence suggested a date of >350 Ka (Bischoff et al. 2003). More recent sampling from the same speleothem points to an age for the fossils of ca. 530 Ka (Bischoff et al. 2007).

Two of the Sima adults provide estimates for brain size. At close to 1,100 cm^3, SH 5 is rather small, but SH 4 with a capacity of 1,390 cm^3 is one of the largest of all Middle Pleistocene specimens. The crania are primitive in some respects, and the massive face of SH 5 is surmounted by a prominent browridge. Vault bones are thickened, and both sagittal keeling and an angular torus are variably developed. The braincase is broadest in the supramastoid region or just above the ear openings. As do their European and African contemporaries, the Sima hominins also exhibit derived traits in the face, shape of the squamous temporal, proportions of the occipital bone, and structure of the cranial base.

An important question is the extent to which these people resemble the later Neanderthals of Europe. As described by Arsuaga et al. (1997), the midface of SH 5 seems to anticipate the distinctive morphology associated with Late Pleistocene Europeans. The infraorbital surface and the side wall of the nose meet at a shallow angle, so as to produce a slight concavity. The cheek region is thus not “inflated” in the extreme manner of Neanderthals, but it can be interpreted as intermediate in form. Also in the Sima sample, continuity of the supraorbital tori at glabella is said to be reminiscent of Neanderthals, and the broad nasal bones are set in a relatively horizontal orientation. At the rear of the cranium, the suprainiac area is large but not very depressed. This trait and the shape of the occipital torus may also foreshadow the Neanderthal condition. How these features are evaluated (whether any of them can be judged to be true Neanderthal apomorphies) will determine how the Sima hominins as well as Arago and Petralona are related to populations outside of Europe and how these regional paleodemes should be treated in phylogenetic schemes.

The TD6 Assemblage from Gran Dolina, Atapuerca

Additional evidence bearing directly on the first peopling of Europe is accumulating from another site in the Atapuerca region. Excavations at Gran Dolina have uncovered stone core-choppers and flakes, animal bones, and human remains dating to the end of the Early Pleistocene. An age slightly in excess of 780 Ka for the TD6 level containing the fossils now seems to be established (Falguères et al. 1999). Cranial specimens include a juvenile face, an adult cheek bone, part of a subadult frontal with some of the brow, and a piece of the cranial base on which most of the joint cavity for the mandible is preserved. There are also broken lower jaws with teeth, along with vertebrae, ribs, and bones of the hand and foot.

Arsuaga et al. (1999b) argue that the TD6 people are not *H. erectus*. Morphology of the hollowed cheek region, vertical orientation of the nasal aperture, features of the hard palate, form of the developing (but already substantially thickened) brow, a wide frontal, the shape of the temporal bone at the side of the vault, and the apparently modern mandibular joint all suggest that the Gran Dolina fossils are different from *H. erectus* and more like later humans. Also, there can be little doubt that this population is distinct from the later Neanderthals. The hollowed cheek (bearing a "canine fossa") points toward this conclusion, and neither in the juvenile nor in the adult faces is there much sign of the specialized Neanderthal condition. One partial mandible is generalized in its morphology, while the teeth resemble those of European and African Middle Pleistocene hominins.

Given this complex of traits, the Gran Dolina material may represent a new species. The name *H. antecessor* was proposed by Bermúdez de Castro et al. (1997). However, the number of fossils is still quite small, and several of the craniodental remains are fragmentary and/or subadult. A fair question is whether there is presently enough evidence to separate the TD6 assemblage from other penecontemporary fossils already on record. In particular, it must be asked whether the Gran Dolina bones and teeth differ from those of other early Europeans such as Mauer, Arago, and the Sima de los Huesos. Much attention has been focused on the development of a "canine fossa" in the midface. Hollowing is indeed apparent in the cheek of the TD6 juvenile, but a fossa is less obvious in the TD6 adult. This feature is variable in its expression in other populations, and the significance of this pattern is unclear. In the mandible, teeth, and postcranial bones, there seem to be few traits that differentiate the Gran Dolina hominins from Europeans of the Middle Pleistocene.

South Asia and the Far East

One South Asian locality deserving mention is the Narmada Valley in central India (Fig. 1). Part of a cranium was found there in 1982, embedded in a conglomerate containing animal bones and a scattering of Acheulean artifacts. Dates for this material are poorly constrained, but it is probably of Middle Pleistocene age (Sonakia and Biswas 1998). Unfortunately the skull is damaged and lacks most of the face. Narmada has been described by its finders as *H. erectus*, but it is better compared to *H. heidelbergensis* (Kennedy et al. 1991). In its overall morphology, the cranial vault is not very different from the African and European hominins already discussed.

Early humans occupied China before 1.6 Ma (Zhu et al. 2004). This part of Asia has been a focus of research in paleoanthropology for quite a long time. Apart from the famous discoveries of *H. erectus* at Zhoukoudian, there are important sites dating to the later Middle Pleistocene. One is Dali and another is Jinniushan, both of them in northern China. The Dali cranium was found in river terrace deposits with stone flakes and fauna. The Jinniushan skeleton was recovered from cave fill containing animal bones but no artifacts. ESR and U-series dates obtained from animal teeth suggest ages of perhaps 300–200 Ka.

Dali is much of a cranium, damaged on the right side and at the base. The alveolar process and palate have been crushed upward. The specimen is otherwise undistorted and carries a lot of information. It has most often been described as "archaic" *H. sapiens*, intermediate in form between *H. erectus* and recent humans. Indeed, there are similarities to *erectus*, and these include the heavy brow, a long low vault that is broad across the base, and the sharply angled occiput. The temporomandibular joint cavity is offset laterally, and the cranial bones are thickened. These traits are best described as primitive retentions. At the same time, Dali exhibits other advanced features that link it to later populations. There is not much postorbital constriction, and the parietal walls are vertical rather than inward sloping. Both the high temporal squama and the proportions of the occiput depart from the *erectus* condition. The face is particularly short and non-prognathic (Wu and Athreya 2013).

The Jinniushan cranium has been reconstructed several times, and there are gaps in the face, the frontal region, and the base. The brow is somewhat less massive than in Dali, but there is an eminence behind bregma, and the occiput is flexed. In other respects, the specimen differs from *H. erectus*. Brain volume is close to 1,300 cm^3. The border of the nasal aperture is vertical (rather than angled forward), and the nasal sill is crested. On the palate, the incisive canal opens anteriorly (just behind the incisor roots) as in recent humans.

In many anatomical details, both Dali and Jinniushan are like other Middle Pleistocene hominins from Africa or Europe. Comparisons based on facial measurements show that the Chinese specimens resemble Broken Hill to about the same extent as does Arago 21 (Rightmire 2001). There are some differences relative to Broken Hill, particularly in upper facial height (reduced in Dali and Jinniushan) and flattening below the nose (more pronounced in Jinniushan). Also, the Dali cheek exhibits a "canine fossa." This feature has been taken as a basis for regarding the Chinese fossil(s) as distinct from western populations, but in fact hollowing of the infraorbital surface can be documented for faces outside of the Far East. Finds from Gran Dolina suggest that this feature may appear in Europe at the beginning of the Middle Pleistocene (section "The TD6 Assemblage from Gran Dolina, Atapuerca"). The recognition of such variation will make it harder to argue for isolation of the major Old World geographic provinces.

Brain Size, Encephalization, and Speciation

Many of the Middle Pleistocene hominins have brains that are enlarged relative to those of *H. erectus*. For 10 of the more complete crania including Bodo, Broken Hill, Petralona, two of the Sima de los Huesos adults, Dali and Jinniushan, average capacity is 1,206 cm^3. For 30 *H. erectus* individuals, the mean volume is only 973 cm^3. This difference is substantial, and it can be determined that a number of the Middle Pleistocene specimens actually lie beyond the limits predicted for an average *H. erectus* of comparable antiquity. Apparently, the change in brain size is not simply a consequence of larger body mass (Rightmire 2004).

Encephalization quotients (EQ) can also be obtained for a number of the specimens. This entails first estimating body mass from orbital height (following Aiello and Wood 1994) and then deriving EQ from the relationship of brain weight to body mass established for mammals by Martin (1981). Here, there are various complications. Apart from the error associated with any weight estimate, there is the fact that the regression equations of Aiello and Wood (1994) are based on several species. Because EQ is a function of body mass predicted for individuals using an interspecific equation, comparisons of the EQ values determined for fossils may be misleading (Smith 2002). In any event, six *H. erectus* crania from Africa and Asia are complete enough to supply the necessary measurements, and the average EQ is 3.61 (Rightmire 2004). This result is comparable to that reported by Ruff et al. (1997), who employ mean estimates of brain and postcranially based body masses to compute EQ values of 3.40 and 3.46 for temporally defined (Early Pleistocene to early Middle Pleistocene) assemblages.

During the balance of the Middle Pleistocene, a rise in EQ is apparent. Bodo and Broken Hill remain within the range observed for *erectus*, but other individuals have higher values and the average for eight specimens is 5.26. The magnitude of this increase is greater than that determined by Ruff et al. (1997) for humans of mid-Quaternary age. These authors use unmatched brain and body weights (means for samples of disassociated crania and postcrania) as a basis for their EQ calculations, and this may account for some of the difference in results. Also, orbit height may tend to underestimate body mass in comparison to predictor variables drawn from the postcranial skeleton. Nevertheless, there is evidence for a shift in brain size at or just before the onset of the Middle Pleistocene.

This increase in encephalization seems to be linked to an episode of speciation. It is generally assumed that the larger brain and accompanying changes to the vault and face distinguish *H. heidelbergensis* from *H. erectus*. Here, an important question must be raised. Differences in frontal proportions, the parietal arc, form of the temporal squama, and rounding of the occiput may be related to the expanding brain, as may the increase in cranial height. As a consequence, traits such as parietal length and occipital curvature are not independent, and it will be incorrect to claim that each of these measurements adds new information useful in phylogenetic analyses. If this is the case, it may not be reasonable to recognize one or more new species, primarily on the strength of an increase in cranial capacity. Examined critically, the morphological evidence may not justify the recognition of so many taxa within *Homo* (Lieberman and Bar-Yosef 2005).

Correlation analysis provides information about the interactions of brain volume with vault form in Pleistocene *Homo* (Rightmire 2012, 2013). It can be determined that the expanding brain influences vertex height and probably also parietal sagittal length. However, brain size fails to influence vault breadth within either *H. erectus* or the Middle Pleistocene hominins. Instead, the cranial base has a major effect on variations in width. Endocranial volume is not associated with the frontal flattening that is so characteristic for *H. erectus*. In *H. erectus*, and in individuals such as Bodo and Petralona, the massive face seems to override the brain as a determinant of frontal form. Encephalization does not explain the occipital rounding that distinguishes Broken Hill, Omo 2, and the Sima crania. Evidently, apart from greater vertex height, few of the vault characters considered diagnostic for *H. heidelbergensis* can be attributed directly to changes in the brain. Traits that are independent can be used to document speciation.

Phylogenetic Hypotheses

Discoveries of new fossils, reassessments of specimens found earlier, and advances in the application of dating techniques show that hominins differing from *H. erectus* appeared in southern Europe before 780 Ka and in Africa at about the same time. One reading of the record suggests that these European and African groups share a number of derived features of the cranial base and vault. Other similarities to later humans are apparent in the facial skeleton (orientation of the nasal aperture, location of the palatal incisive canal) and perhaps the mandible (symphyseal height increased relative to the posterior corpus, incipient mental eminence). Postcranial bones known principally from the Sima de los Huesos in Spain suggest that the European hominins were heavily built, perhaps reflecting adaptation of body form to a temperate environment. In sum, the anatomical evidence can be interpreted as supporting a claim that all of the earlier Middle Pleistocene fossils belong to a single lineage (Fig. 4a). This species can be called *H. heidelbergensis*. Later in the Middle Pleistocene, some populations dispersed northward within Europe, where they were subject to long episodes of extreme cold. During glacial advances and retreats occurring over several hundred thousand years ago, these hominins continued to adapt to harsher (cold/dry) conditions and evolved the specialized craniofacial characters and body build of the Neanderthals. In this same interval of time, other representatives of *H. heidelbergensis* in Africa were becoming more like modern humans. Fossil finds from Irhoud in Morocco, the Omo in southern Ethiopia, Herto in the Middle Awash region, and Laetoli in Tanzania document this evolutionary progression toward *H. sapiens*.

Alternatively, it can be argued that *H. antecessor* is the ancestor to all later humans (Fig. 4b). This species is considered to be descended from (African) *H. erectus* (Bermúdez de Castro et al. 1997). Rather soon after its first appearance in Spain, *H. antecessor* must have given rise to *H. heidelbergensis*. In this scenario, the *heidelbergensis* lineage was confined exclusively to Europe, where its members gradually acquired the large nose, more projecting facial skeleton, and other morphology of the Neanderthals. This is the accretion hypothesis of Dean et al. (1998). Also, *H. antecessor* is presumed to have evolved an African offshoot, represented at localities such as Bodo, Broken Hill, and Elandsfontein. Although these Middle Pleistocene hominins are acknowledged as morphologically similar to (perhaps even capable of exchanging genes with) their European contemporaries, they are not assigned to *H. heidelbergensis*. Instead, the African fossils are lumped

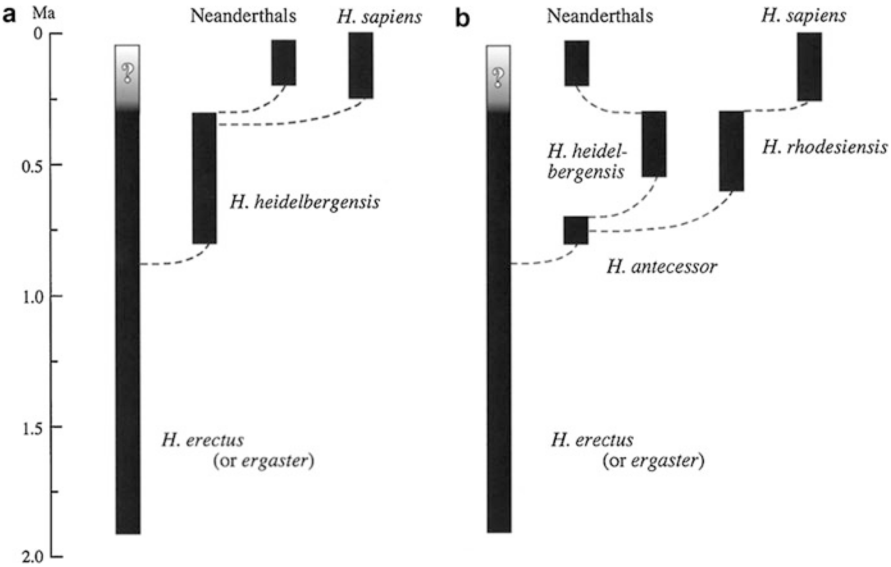

Fig. 4 Alternative evolutionary trees showing the relationships among *H. erectus*, Middle Pleistocene hominins, Neanderthals, and modern humans. Bars depict the time range estimated for each species. Broken lines indicate likely links of ancestors with descendants. Hypothesis (**a**) shows *H. heidelbergensis* to be descended from *H. erectus*. This species must have dispersed widely across Africa and western Eurasia at the beginning of the Middle Pleistocene, and some populations may also have reached the Far East. Here *H. heidelbergensis* is depicted as the antecedent to both Neanderthals in Europe and recent humans all across the old World. In a different interpretation (**b**), *H. antecessor* is recognized as the direct descendant of *H. erectus*. In turn, *H. antecessor* evolved into European *H. heidelbergensis*, and this species gave rise (only) to the Neanderthals. African *H. rhodesiensis* is considered to be ancestral to *H. sapiens*

in a separate species, for which the nomen *H. rhodesiensis* is available. Whether this taxonomic view can be accepted will depend largely on the outcome of excavations that are continuing in the TD6 levels at Gran Dolina. It will be important to expand the sample of fossils documenting the earliest European settlers.

Another question is whether the far eastern specimens can be accommodated within one of these systematic frameworks. The answer is a tentative yes, although the evidence is sparse. Dali and Jinniushan do share a number of apomorphic traits with the western hominins. But there are some differences, and the face has been a focus of contention. Dali has a short face, and this would be true even if damage to the maxilla were corrected. Jinniushan also has a short clivus (the subnasal portion of the maxilla), and it is oriented vertically. In Dali, there is hollowing of the cheek below the orbit, and such excavation is not present in the African crania. Much has been made of this facial morphology, but in fact there is individual variation (see section "Brain Size, Encephalization, and Speciation"). The significance of the Dali “canine fossa” should not be overemphasized. It is possible to argue that the later Middle Pleistocene hominins of China document an eastward excursion of *H. heidelbergensis*, where this species is taken to be the link between *H. erectus* and all later humans. Dating is not very firm, but probably fossils such as Dali and Jinniushan are younger than those in Africa. This may suggest that *H. heidelbergensis* was a late arrival in the eastern part of Asia.

Current Debates

A differing interpretation arises from ongoing analyses of the discoveries at the Sima de los Huesos. As noted above, the Sima skulls exhibit traits expected to occur (very) early in the evolution of the Neanderthal lineage (Arsuaga et al. 1997). Recently, it has been emphasized that the Sima de los Huesos teeth are remarkably like those of “typical” Neanderthals (Martinón-Torres et al. 2012). The upper incisors display conspicuous labial convexity and a distinctive shovel shape, while the upper premolars present a bulging of the buccal aspect of the crown. The M^1s possess an enlarged hypocone, giving the crown a rhomboidal outline characteristic of Neanderthals. The P_3s have a symmetrical contour. Here, the talonid is reduced or absent, so that the remaining cusps occupy a small area near the lingual border of the crown. This Neanderthal-like morphology is more pronounced in the Sima sample than in other Middle Pleistocene hominins. Indeed, Martinón-Torres et al. (2012) claim that the Sima specimens are “more Neanderthal” in form than the Mauer or the Arago dentitions. They suggest that the Sima may constitute a source population for Neanderthals, while Mauer and Arago document the presence of a morphologically distinct lineage. Such a conclusion is favored by Stringer (2012), who envisions two species coexisting in the European Middle Pleistocene. The second species (*H. heidelbergensis*) includes fossils presumed to predate the evolutionary emergence of *H. neanderthalensis*, as well as specimens such as Petralona from later time periods.

Archaeology and Behavior in the Middle Pleistocene

Controversy over the number of Middle Pleistocene lineages in Eurasia and Africa will likely continue. Nevertheless, it is becoming clear that the hominins were more encephalized than *H. erectus*. Also, there is evidence from archaeology that these people were developing new behavior. Later Acheulean artifacts are known from numerous African sites, including Bodo, Olorgesailie, Isimila, Lake Ndutu, the Cave of Hearths, Elandsfontein, and Duinefontein 2. In general, later Acheulean hand axes can be characterized as thinner, more symmetrical, and bearing many more flake scars than their earlier counterparts. In some sites, relatively small hand axes are accompanied by flake tools resembling those of the Middle Stone Age (Klein 2000). While it is dangerous to expect universal associations of *Homo* species with particular industrial traditions, informative patterns may be uncovered (Foley and Lahr 1997). In virtually all mid-Quaternary African contexts, where diagnostic human bones are found with later Acheulean artifacts, the maker is *H. heidelbergensis* (or *H. rhodesiensis*). One may conclude that this species was capable of producing a tool kit more sophisticated than that utilized routinely by *H. erectus*.

In western Eurasia, hominins equipped with Acheulean tools were present by the onset of the Middle Pleistocene (780 Ka) at Gesher Benot Ya'aqov in Israel (Goren-Inbar et al. 2000). Farther to the west in Europe, there are no Acheulean sites from the beginning of the Middle Pleistocene, but Boxgrove in Britain is likely to be 500 Ka in age. This locality has yielded thin, extensively flaked flint bifaces, along with bones of horses and rhinoceroses bearing cut marks. The animals may well have been hunted and butchered. In addition, there is the shaft of a human tibia. The dimensions of this bone at midshaft are large, and the Boxgrove individual was probably quite massive. This hominin has been attributed to *H. heidelbergensis* by Roberts et al. (1994). Signs of later Acheulean toolmakers are known from Torralba and Ambrona in Spain, where the artifacts are again found with large herbivores, including elephants and horses (Freeman 1994). Acheulean artifacts occur also at several sites in France and Italy. At Castel di Guido in central Italy, finely flaked bifacial tools were produced from elephant bone (Villa 1991). At some other earlier Middle Pleistocene localities, including Arago Cave, the stone industries contain small chopping tools and flakes but no hand axes (De Lumley et al. 1984). The reasons for this difference are unclear, but the availability of suitable raw materials, the constraints imposed by different types of stone, and the context in which tools were manufactured must all be considered, along with the possibility that distinct cultural behaviors or styles are represented.

An isolated but particularly significant example of the skills acquired by mid-Quaternary Europeans comes from Schöningen in Germany. Eight carefully crafted wooden throwing spears have been uncovered near a former lake, where they are associated with flint tools and chips (Thieme 1997, 2005, 2007). Scattered through the same horizon are the remains of numerous horses. Many of the bones are cut-marked, and some of the animals must have been processed for meat and marrow extraction (Roebroeks 2001). More convincingly than other early European assemblages, the Schöningen discovery points to systematic hunting of large animals. Stalking and killing of agile or dangerous prey requires experience and practice, and it is reasonable to hypothesize that the people were cooperating with one another in these efforts. Increased levels of social cooperation and exchange of knowledge would have become the norm. And if the hunters at Schöningen (also at sites such as Boxgrove and Arago) were able to obtain large amounts of meat, they would likely have shared or exchanged food with other groups, perhaps at established meeting places (Roebroeks 2001). Certainly our understanding of the behavior of the early Europeans remains quite incomplete, but it is apparent that bands of *H. heidelbergensis* were not only skilled at flaking stone but also capable of interacting regularly in the pursuit of game and other social activities.

Conclusion

Middle Pleistocene crania from Bodo, Broken Hill, Elandsfontein, and Lake Ndutu in Africa are quite similar to penecontemporaneous fossils from Europe. Craniodental remains and jaws from Petralona and Arago Cave are particularly informative, and the assemblage from Sima de los Huesos is spectacular. If this grouping is expanded to include the Mauer mandible, then it can be argued that *H. heidelbergensis* was a geographically dispersed paleospecies.

A question is whether additional specimens from China can be accommodated within this taxon. Dali and Jinniushan share a number of apomorphic traits with the western hominins, but there are differences, and the face has been a focus of contention. Dali has a short face, and there is hollowing of the cheek below the orbit. Probably the significance of the Dali "canine fossa" should not be overemphasized. Later Middle Pleistocene populations of China may document an eastward excursion of *H. heidelbergensis*, where this species is taken to be the link between *H. erectus* and all later humans.

Homo heidelbergensis differs from *H. erectus* in absolute as well as relative brain size. Correlation analysis provides information about the interactions of brain volume with vault form. It can be determined that the expanding brain influences vertex height and probably also parietal sagittal length. Traits that vary independently from brain volume have greater taxonomic utility and include anterior frontal broadening, perhaps the high, arched outline of the temporal squama, and lateral expansion of the parietal vault. Encephalization does not explain the occipital rounding that distinguishes Broken Hill, Omo 2, and the Sima crania, nor does it account for the greater elevation of the lambda-inion chord. Traits of the cranial base also serve to diagnose *H. heidelbergensis* in relation to *H. erectus*. Morphology of the temporomandibular joint generally resembles that in *H. sapiens*, as is the case for the tympanic and petrous portions of the temporal bone. There is no reduction in overall face size in comparison to *H. erectus*, and the facial skeleton seems to be "hafted" to the braincase in such a way as to accentuate anterior projection. But reorientation of the nasal aperture and forward placement of the incisive canal within the palate suggest that the face of *H. heidelbergensis* may be more nearly vertical, as in *H. sapiens*.

Later Acheulean artifacts are known from many mid-Pleistocene African localities, and in general, the hand axes can be characterized as thinner and more symmetrical than earlier examples. In some sites, relatively small hand axes are accompanied by flake tools resembling those of the Middle Stone Age. While it is dangerous to expect universal associations of *Homo* species with particular industrial traditions, in virtually all African contexts where diagnostic human bones are found with later Acheulean artifacts, the maker is *H. heidelbergensis*. One may conclude that these people were more advanced in behavior than their predecessors. There is evidence that *H. heidelbergensis* was able to make relatively sophisticated stone tools, hunt larger and more dangerous game animals, and perhaps engage in cooperative social activities.

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Neanderthals and Their Contemporaries

Katerina Harvati

Contents

K. Harvati (✉)
Paleoanthropology, Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany
e-mail: katerina.harvati@ifu.uni-tuebingen.de; monika.doll@ifu.uni-tuebingen.de

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Abstract

Neanderthals are the group of fossil humans that inhabited Western Eurasia from the mid-Middle Pleistocene until ca. 40 Ka ago, when they disappeared from the fossil record, only a few millennia after the first modern humans appear in Europe. They are characterized by a suite of morphological features that in combination produce a unique morphotype. They are commonly associated with the Mousterian lithic industry, although toward the end of their tenure they are sometimes found with assemblages resembling those produced by early modern humans. Although there is still discussion over their taxonomic status and relationship with modern humans, it is now commonly recognized that they represent a distinct, Eurasian evolutionary lineage sharing a common ancestor with modern humans in the Middle Pleistocene. This lineage is thought to have been isolated from the rest of the Old World, probably due to the climatic conditions of the glacial cycles. Glacial climate conditions are often thought to have been at least in part responsible for the evolution of some of the distinctive Neanderthal morphology, although genetic drift was probably also very important. The causes of the Neanderthal extinction are not well understood. Worsening climate and competition with modern humans are implicated.

The Discovery of Neanderthals: Historical Background

Although the first Neanderthal remains were discovered in the early nineteenth century (Engis child in 1830, Forbes Quarry adult in 1848), it was not until the discovery of the skeleton from the Neander Valley in 1856, roughly coinciding with the publication of Darwin's "The Origin of Species" in 1859, that the existence of an extinct kind of archaic humans was recognized. It is this locality that lends its name to the group, and it is there that the debate surrounding the relationship of Neanderthals with modern humans began.

The antiquity of the Neanderthal skeleton and its status as an archaic human was not immediately accepted. Instead, its peculiar anatomical attributes were considered the result of various pathologies, including rickets. Its antiquity was only firmly established with the eventual discovery of additional skeletons of similar morphology associated with lithic artifacts and extinct fauna.

Neanderthals were assigned to the species *H. neanderthalensis* as early as 1864 (King 1864). However, once their status as archaic predecessors of modern humans was accepted, their relationship with modern humans, and particularly modern Europeans, began to be intensely debated. The predominant view in the 1910s and 1920s was represented by scientists like Marcellin Boule and Sir Arthur Keith, who were among the most influential scholars of their day. They placed Neanderthals in their own species and rejected any ancestral role for them in the evolution of modern people, pointing out their "primitiveness" and presumed inferiority (Boule 1911/1913; Boule and Vallois 1957).

This perception of Neanderthals began to change during the 1930s. A rearrangement and "pruning" of the tangled hominin taxonomy was undertaken in the 1940s and 1950s by Mayr, Simpson, and Dobzhansky, who placed Neanderthals and other Middle Pleistocene fossil specimens within our own species, *Homo sapiens*. According to this view, Neanderthals were thought to have evolved into modern people through anagenetic evolution (Trinkaus and Shipman 1992, 1993; Tattersall 2000). This view has been reexamined in more recent years, with new evidence coming from modern human and fossil genetic studies, the development of better dating techniques and new approaches to the analysis of morphology. Currently, Neanderthals are commonly viewed as a distinct, Western Eurasian evolutionary lineage, which probably did not contribute significantly to the evolution of modern people.

Chronological Distribution

The earliest human skeletal remains found in Europe have been recovered from Sima del Elefante in Atapuerca, Spain, dated to ca. 1.2 Ma (Carbonell et al. 2008) and from Barranco León, with a possibly even earlier date (up to 1.4; Toro-Moyano et al. 2013; but see Muttoni et al. 2013). Human remains dated to ca. 800 Ka have been recovered from Gran Dolina (Atapuerca, Spain; Bermúdez de Castro et al. 1997; Falguères et al. 1999), and lithic artifacts dated to ca. 700 and possibly up to 950 Ka have recently been discovered in England (Parfit et al. 2005, 2010) documenting an early human presence also in Northern Europe. These early European populations are considered by some to have been ancestral to the later, Middle Pleistocene Europeans and to Neanderthals (e.g., Bermúdez de Castro et al. 1997), but may also represent unsuccessful early episodes of colonization that ended in local extinctions. A calvaria from Ceprano, Italy, previously thought to date to ca. 780–800 Ka (Manzi et al. 2001) has recently been redated to ca. 450 Ka (Muttoni et al. 2009) and is now referred to *Homo heidelbergensis* (Mounier et al. 2011).

The first appearance of Neanderthals in the fossil record is not clear-cut. Neanderthal-like features appear for the first time in a mosaic fashion in Middle Pleistocene European humans, as, e.g., in the large assemblage from Sima de los Huesos (Atapuerca), Spain (Arsuaga et al. 1997), recently dated to between 400 and 600 Ka (Bischoff et al. 2003, 2007; Arnold et al. 2014; but see Stringer 2012 for criticisms of this age estimate). Different Neanderthal-like traits appear at different times and places and in different combinations, but their presence in the European Middle Pleistocene fossil specimens suggests that the latter were early representatives of the Neanderthal lineage (Fig. 1).

A progressively stronger expression of Neanderthal morphology is perceived through time, with specimens from the late Middle Pleistocene/early Late Pleistocene ($\sim$200–100 Ka) showing clear, albeit still not fully expressed, Neanderthal morphology. The full suite of Neanderthal features appears with the "classic" Neanderthals, in the Late Pleistocene, dated from approximately 70–30 Ka. This group includes

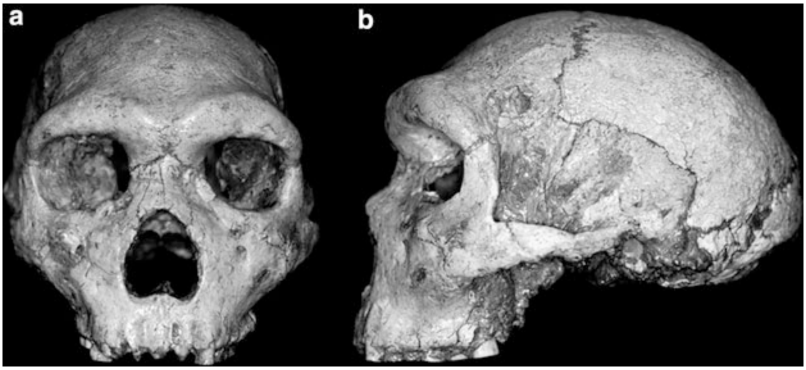

Fig. 1 Frontal (**a**) and lateral (**b**) views of the Middle Pleistocene cranium from Petralona, Greece, showing incipient Neanderthal morphology in its facial region (Courtesy of Eric Delson and © Eric Delson, Photo by K. Harvati)

among others the famous "Old Man" of La Chapelle-aux-Saints, as well as the type specimen from the Neander Valley, Feldhofer 1.

The last date of appearance of Neanderthals, and thus the potential coexistence of Neanderthals and modern humans in Europe, has also been controversial due to methodological issues affecting radiocarbon dating of this period (see Conard and Bolus 2008; Blockley et al. 2008). The radiocarbon chronology of the late Neanderthals throughout Europe has been recently extensively revised using the latest methodological advances. Radiocarbon dates reported here are uncalibrated, unless otherwise specified.

The Neanderthal specimens from Layer G1 at Vindija, Croatia, were recently directly redated to ca. 33–32 radiocarbon Ka BP through direct accelerator mass spectrometry (AMS) using collagen ultrafiltration (Higham et al. 2006), revising previously published younger dates of ca. 29 radiocarbon Ka BP (Smith et al. 1999).

Two sites in France, both associated with the Châtelperronian lithic industry (see below), have been associated with Neanderthal remains. The partial skeleton from Saint-Césaire was originally dated to ca. 36 Ka BP using the thermoluminescence (TL) dating method (Mercier et al. 1991). A recent direct AMS ultrafiltration radiocarbon date on the skeleton produced a somewhat older date of ca. 36 radiocarbon Ka BP (between 41,950 and 40,660 years BP calibrated; Hublin et al. 2012). The Châtelperronian layers containing a subadult Neanderthal temporal bone (Hublin et al. 1996), as well as several Neanderthal isolated teeth (Bailey and Hublin 2006) at Arcy-sur-Cure (Grotte-du-Renne), were originally dated by AMS radiocarbon to ca. 34 Ka (David et al. 2001). Hublin et al. (2012) redated the Châtelperronian and Late Châtelperronian layers at Arcy to between ca. 40 and 35.5 radiocarbon Ka BP using accelerator mass spectrometry radiocarbon dates on ultrafiltered bone collagen (calibrated to between 41,620 and 40,570 years BP).

A very late direct radiocarbon date for one of the Mezmaiskaya (Russia) Neanderthal infants (~29 Ka; Ovchinnikov et al. 2000) is now thought to have resulted from modern carbon contamination. Recent work on this site has produced much older ESR dates (~70–60 Ka for the first infant and ~40 Ka for the second; Skinner et al. 2005), as well as a direct ^{14}C AMS ultrafiltration date on the second infant of ca. 39.7 Ka BP (calibrated to between 42.3 and 45.6 Ka cal BP; Pinhasi et al. 2011).

Several sites in Spain have been proposed as showing late Neanderthal occupation. Zafarraya was until recently considered to be among the youngest Neanderthal sites in Europe. The Neanderthal-bearing layers there had been dated to between ca. 33.4 and 28.9 Ka BP using conventional ^{14}C and uranium series dating (Hublin et al. 1995). The age of these Neanderthal layers has most recently been revised (using ultrafiltration and AMS ^{14}C) to be much older and close to the radiocarbon limit (Wood et al. 2013). A relatively late date for Neanderthal layers at Las Palomas (ca. 34.5 and 35 Ka BP, both AMS ^{14}C on burnt faunal bone; Walker et al. 2008) has been criticized as unreliable due to the difficulties in dating burnt material (Wood et al. 2013). Finally an exceptionally recent date of 24 Ka BP as the date of last appearance of Neanderthals in Iberia based on redating of a Mousterian lithic assemblage (Finlayson et al. 2006) is considered questionable due to stratigraphic inconsistencies (Delson and Harvati 2006) as well as methodological concerns (Wood et al. 2013).

Geographic Distribution

Neanderthals are commonly thought of as European hominins, and Europe is often considered as their geographical area of origin, with specimens outside the continent representing later range expansions (Hublin 1998, 2000). Within Europe, Neanderthals range from Iberia to Russia and from the Mediterranean to Northern Europe. Outside of the continent, their presence has been documented in the Near East and in Western Asia as far east as Uzbekistan (Fig. 2) and Siberia (Krause et al. 2007b).

Eastern Neanderthals are often juxtaposed with those from Western Europe in that their morphology is mosaic in pattern and not fully “Neanderthal” (Vandermeersch 1989; Smith 1991; Rak 1993). In some of their features, Eastern Neanderthals show conditions that have sometimes been perceived as more modern (though not all specimens show the same conditions for the same features), leading some to question the Neanderthal identity of these fossils (Arensburg and Belfer-Cohen 1998). A more widely accepted view is that the weaker expression of Neanderthal traits in these specimens reflects primitive retentions rather than affinities with modern humans (Stringer 1990). Similarly, weakly expressed Neanderthal morphology is found in early Neanderthals, such as those from Saccopastore, again interpreted as retentions of primitive morphology (Condemi 1992).

Morphology

Neanderthals are characterized by a suite of distinctive cranial, mandibular, dental, and postcranial anatomical features (Figs. 3 and 4), some of which represent retentions of ancestral conditions but many of which are derived for this group.

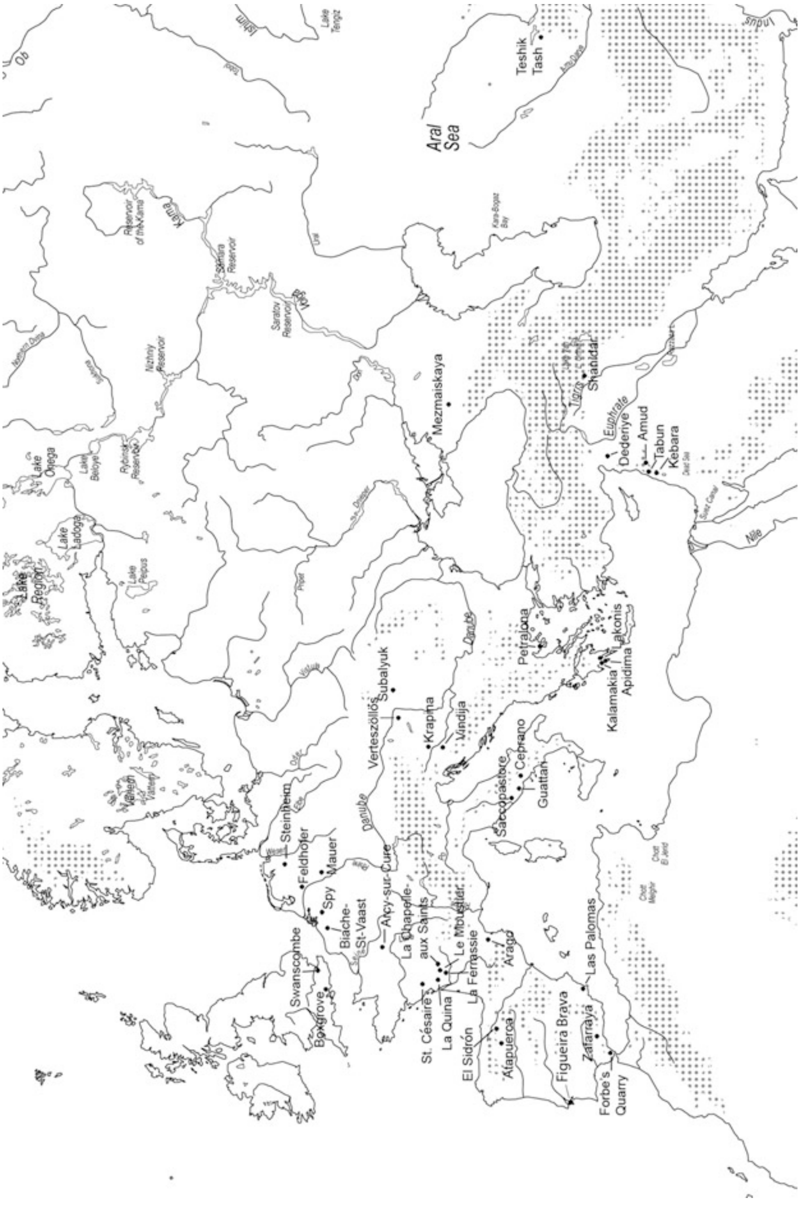

Fig. 2 Map of the geographic distribution of Neanderthals, showing several sites preserving Neanderthal and pre-Neanderthal skeletal remains discussed in the text

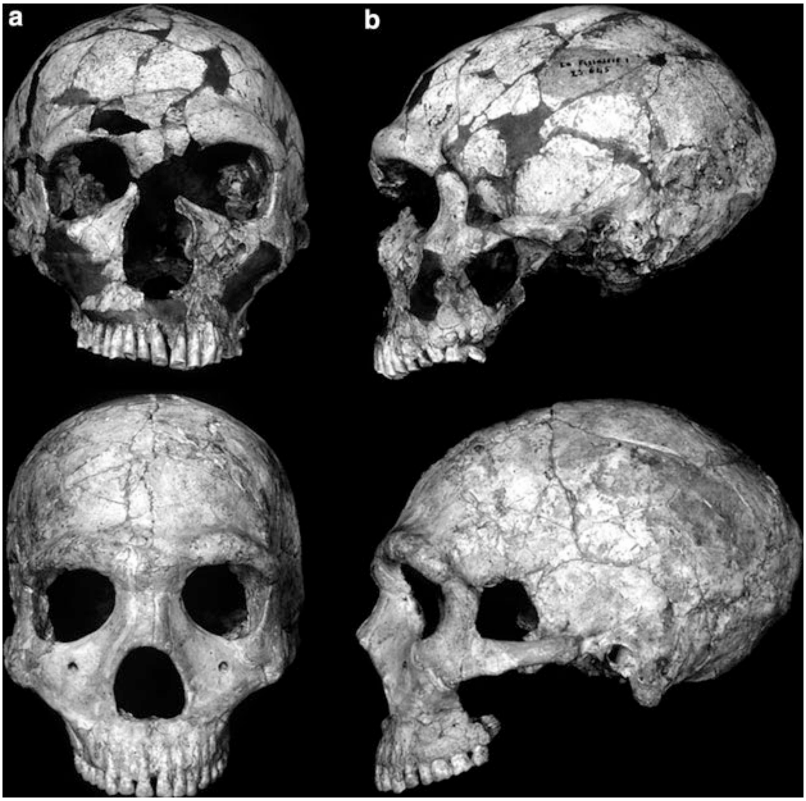

Fig. 3 Frontal (**a**) and lateral (**b**) views of the La Ferrassie 1 (*top*) and Amud 1 (*bottom*) Neanderthal crania (Courtesy of Eric Delson, © Musée de l' Homme and Rockefeller Museum, Photo by C. Tarka for Ancestors)

Primitive traits, shared with the common ancestor of both Neanderthals and modern humans, include their low and elongated crania, heavy brow ridges, large faces with large nasal apertures, and the lack of a chin. Neanderthals share some derived features with modern humans, including enlarged brains, reduced prognathism, a weak occipital torus, and a longer and more rounded occipital. A list of proposed deriver traits is provided in Table 1.

A detailed morphological description of the various anatomical areas follows.

Cranium

Face

The Neanderthal face is characterized by a heavy, double-arched supraorbital torus which does not show distinct elements and grades smoothly onto the frontal squama. The orbits are large and rounded. The nasal aperture is very large and

Fig. 4 Complete Neanderthal skeleton (*left*) reconstructed using elements from five partial skeletons (principally La Ferrassie 1 and Kebara 2) compared to a modern human skeleton (*right*) (Courtesy of Ian Tattersall and Gary Sawyer, Photo by Ken Mowbray)

broad. The nasal cavity is voluminous and displays large medial projections and a bilevel internal nasal floor. Neanderthals show pronounced midfacial prognathism and an oblique and inflated infraorbital plate with no canine fossa, which obliquely recedes into the zygomatic bone. The inferior root of the zygomatic is oblique, and not sharply angled, and the zygomatic processes are elongated and thin. Internally, the maxillary sinuses are large, while the frontal sinus is expanded laterally to fill most of the supraorbital torus (up to midorbit) but does not extend upward into the frontal squama (Heim 1974, 1976; Stringer et al. 1984; Rak 1986; Trinkaus 1987, 2003; Schwartz and Tattersall 1996a; Arsuaga et al. 1997; Franciscus 1999, 2003).

Several alternative hypotheses have been proposed to account for the distinctive Neanderthal facial morphology. The large nasal aperture and associated structures have been proposed to relate to cold-climate adaptation and to function in warming and humidifying inspired air, as well as to dissipate heat (Coon 1962; Dean 1988). Another interpretation sees the Neanderthal facial features as biomechanical consequences of intense paramasticatory behavior evidenced by the unusual anterior tooth wear pattern exhibited in this fossil group (Heim 1976; Rak 1986; Trinkaus 1987). Among recent humans, the shape of the nasal cavity has been shown to be affected by climatic factors such as temperature and humidity (Noback et al. 2011).

Table 1 Some proposed derived Neanderthal features (Adapted from Hublin (1998))

Cranium
Midfacial prognathism
Medial nasal projections above a spinoturbinal crest delineating a prenasal fossa
Double-arched supraorbital torus with no distinct elements
Horizontally flat or convex infraorbital area, obliquely receding in alignment with the anterolateral surface of the zygomatic bone
Secondarily increased relative platycephaly
"En bombe" cranial shape
Highly convex occipital plane (chignon or occipital "bun")
Pitted suprainiac fossa associated with a bilaterally protruding occipital torus
External auditory meatus at the level of the posterior zygomatic arch, with a strong inclination of the basal groove of this process
Flat mandibular fossa
Long and narrow foramen magnum
Laterally flattened, small mastoid process and large juxtamastoid eminence
Anterior mastoid tubercle
Small and inferiorly positioned posterior semicircular canal
Mandible
Mental foramen below the M_1
Retromolar gap
Asymmetric mandibular notch, coronoid process higher than the condyle
Laterally expanded condyle
Oval/horizontal shape of the mandibular foramen
Large pterygoid tubercle
Dentition
Expanded anterior dentition
Taurodontism
Mid-trigonid crest on mandibular molars
Markedly skewed upper molar crowns
Asymmetric mandibular fourth premolar crown

However, large noses and nasal cavities are characteristic of warm-climate populations, although tall nasal apertures characterize arctic populations (Hubbe et al. 2009), making the climatic adaptation hypothesis difficult to evaluate. On the other hand, several studies have rejected the proposed biomechanical advantages of the Neanderthal face (Antón 1994, 1996). A third interpretation considers Neanderthal facial morphology as primarily the result of stochastic processes (Hublin 1998; Weaver et al. 2007).

Vault

Neanderthals show a particularly flat and elongated vault in lateral profile and an "en bombe," rounded profile in posterior view, with the widest point at the mid-parietals. The occipital region shows a highly convex occipital scale, with a flattening above lambda, termed occipital "bun" or "chignon." The occipital torus is weak with no external occipital protuberance. It is inferiorly undercut by the nuchal plane, but not clearly defined superiorly, and shows a pitted oval depression above it (suprainiac fossa). The temporal squama is superoinferiorly low, anteroposteriorly short, and symmetrically arched. The external auditory meatus is elevated relative to the zygomatic process and the floor of the glenoid fossa. The parietomastoid suture is relatively long and straight (Boule 1911/1913; Hublin 1978, 1988a, b, 1998; Stringer et al. 1984; Condemi 1988; Lieberman 1995; Schwartz and Tattersall 1996b; Dean et al. 1998; Harvati 2003b).

Neanderthal endocasts show similar features to those of modern humans (Holloway 1985), but their average cranial capacity is larger measuring approximately 1,520 cm^3 (from 1,200 to 1,700 cm^3). Large brains might be related to cold-climate adaptation in these hominins (Churchill 1998). Even though absolute brain size was larger on average in Neanderthals relative to modern humans, their relative brain size may have been smaller due to their greater body mass (Ruff et al. 1997). The brain enlargement characteristic of both Neanderthals and modern humans appears to have followed distinct evolutionary trajectories in the two lineages, with Neanderthals retaining an archaic endocranial shape despite larger size, and modern humans exhibiting distinct shape, as well as size, changes (Bruner et al. 2004). Modern human endocasts show enlarged parietal lobes, as well as expanded temporal lobes and enlarged cribriform plates compared to Neanderthals (Bruner et al. 2004; Bastir et al. 2011). The distinctive globular shape of the human endocast appears to be achieved early in development, through the addition of a distinct "globularization" phase (Gunz et al. 2010).

Basicranium

The mastoid process is small and equal in size to or smaller than the juxtamastoid eminence. It often shows a mastoid tubercle. The petrotympanic crest originates at the most inferiorly projecting part of the tympanic, and the tympanic plate is coronally oriented. The mandibular fossa is wide, shallow, and medially closed off. The foramen magnum is long, narrow, and ovoid in shape. The cranial base is relatively flattened. Recent examination of the internal morphology of the inner ear using computer tomography (CT) scans has revealed a distinctive shape for the Neanderthal bony labyrinth, most significantly characterized by an inferior placement of the posterior semicircular canal (Vallois 1969; Santa Luca 1978; Laitman and Heimbuch 1982; Trinkaus 1983; Stringer et al. 1984; Stringer 1985; Vandermeersch 1985; Hublin 1988; Condemi 1991, 1992; Elyaqtine 1995; Hublin et al. 1996; Schwartz and Tattersall 1996b; Harvati 2003b; Spoor et al. 2003).

Mandible

Neanderthal mandibles show a receding symphysis resulting in the absence of a mental eminence or chin. There is a space between the third molars and the ascending ramus, termed the retromolar gap. Recent analyses have shown this trait to be related to increased size in modern humans, great apes, and Middle-Late Pleistocene

European fossils, suggesting caution in the interpretation of its derived status. The Neanderthal mental foramen is positioned posteriorly below the first mandibular molar rather than the premolars, unlike modern humans. The gonial area is rounded. The mandibular (sigmoid) notch is shallow and asymmetric with a coronoid process that is higher than the condyle. The mandibular notch meets the condyle in a medial position, and the condyle is laterally expanded. The submandibular and pterygoid fossae are very deep, and the mandibular foramen shows an oval-horizontal shape (Boule 1911/1913; Vandermeersch 1981; Stringer et al. 1984; Tillier et al. 1989; Condemi 1991; Franciscus and Trinkaus 1995; Hublin 1998; Rak 1998; Rosas 2001; Jabbour et al. 2002; Rak et al. 2002; Trinkaus et al. 2003; Rosas and Bastir 2004; Nicholson and Harvati 2006).

Dentition

The dimensions of the Neanderthal posterior dentition completely overlap with those of modern humans. However, Neanderthal anterior teeth, and particularly the incisors, are larger. Neanderthal teeth show enlargement of the pulp chambers (taurodontism), although this trait is variable in its degree of expression and seems to be more weakly expressed in Eastern Neanderthals. Several morphological dental features appear at very high frequencies in Neanderthals compared to modern humans. These include shoveling of the incisors and the presence of a tuberculum dentale; asymmetric lower fourth premolars with transverse crests and distolingual cusps; markedly skewed upper molars; lower molars with mid-trigonid crests; and the absence of four-cusped lower third molars. Finally, the Neanderthal dentition is distinctive in its wear patterns, showing markedly greater wear anteriorly. Although this is not a heritable trait, it has been used to infer behavioral practices (Keith 1913; Trinkaus 1983; Bytnar et al. 1994; Bailey 2002, 2004; Bailey and Lynch 2005; Bailey and Hublin 2006).

Postcranium

The Neanderthal postcranium (Fig. 4) is overall robust, with markedly curved shafts of the femur and radius, thick cortical bone, and strong muscle and ligament markings. Neanderthals were short relative to early modern humans and probably also to earlier *H. ergaster* populations. Estimated stature averages ~169 cm for males and ~160 cm for females. Body mass is estimated at ~78 kg for males and ~66 kg for females. Additional Neanderthal postcranial features include a broad and deep ribcage, with large thoracic volume, especially inferiorly; relatively short distal limb segments; large articular heads of the tibia and femur; a relatively low angle between the femoral neck and shaft; the absence of a pilaster on the femur and a more rounded (in cross section) femoral shaft; a dorsal, rather than ventral, sulcus on the axillary border of the scapula; large and round apical tufts of the manual phalanges and a relatively short proximal thumb phalanx; clavicles showing two curvatures in dorsal view; and an elongated and thin pubic ramus (Boule 1911/1913; Trinkaus 1983; Ruff 1991, 1993, 1994; Holliday 1997a, b; Ruff et al. 1997; Churchill 1998; Rosenberg 1998; Trinkaus and Ruff 1998; Pearson 2000; Voisin 2000; Niewoehner 2001; Franciscus and Churchill 2002; Weaver 2003; Sawyer and Maley 2005).

Several of these traits have been linked to high activity levels and/or cold-climate adaptation. Others could represent Neanderthal-derived features, but since very little is known about their ancestral conditions, no definitive assessments can be made at present. Neanderthal body proportions are commonly viewed as "hyperarctic." It has been suggested that the short stature and short distal limb proportions represent a cold-climate adaptation following Bergmann's and Allen's rules, as seen also in some modern human populations (Trinkaus 1981; Holliday 1997a, b; Steegmann et al. 2002). Overall robusticity, wide trunks, and features of the Neanderthal femur and pelvis have also been linked to climate adaptation (Ruff 1994; Pearson 2000; Weaver 2003). As improved paleoclimatic information suggests that Neanderthal ranges followed favorable climatic conditions, the designation of Neanderthals as "hyperarctic" has been challenged (Finlayson 2004). A recent estimate of the ability of the Neanderthal body shape to withstand cold temperatures showed only a small advantage over early modern humans with a less "cold-adapted" body form (Aiello and Wheeler 2003), indicating that Neanderthals could not have inhabited their high-latitude habitats without substantial cultural insulation.

Life History, Pathology, and Trauma

Neanderthal growth seems in many ways similar to modern humans, although there are indications that some aspects of their development, including brain and dental growth, were accelerated (Dean et al. 1986, 2001; Ramírez Rozzi and Bermúdez de Castro 2004; Smith et al. 2007, 2009, 2010). The age-mortality profile observed among Neanderthals has been found to differ from that of recent human and other mammals in having a low percentage of older adults and infants and a high percentage of adolescents and prime-age adults (Trinkaus 1995). A similar pattern was found in the Atapuerca Sima de los Huesos and Krapina human assemblages (Bocquet-Appel and Arsuaga 1999). Although there are problems associated with such paleodemographic analyses, the observed mortality profile suggests very low adult life expectancy, probably associated with high levels of stress and trauma (Trinkaus 1995). Increased survivorship of adults resulting in a longer lifespan may have appeared very late in human evolution and not until the advent of early modern humans (Caspari and Lee 2004).

Indications of trauma and stress are ample in the Neanderthal skeletal record, so much so that it has been remarked that posttraumatic lesions can be found on almost every well-preserved adult Neanderthal skeleton (Trinkaus 1983; Berger and Trinkaus 1995; Jelinek 1994). An analysis of traumatic lesion patterns in Neanderthals found them to be concentrated in the head and neck region, an uncommon pattern of injury that was argued to result from hunting strategies requiring proximity to large prey animals (Berger and Trinkaus 1995). On the other hand, some injuries have been argued to originate from interpersonal aggression (Trinkaus 1983; Zollikofer et al. 2002; Churchill et al. 2009). As the majority of traumatic lesions in Neanderthals are healed or partially healed, they have also been seen as evidence for social assistance in these hominins, as have the multiple incidents of highly worn or otherwise nonfunctional dentition (Trinkaus 1983, 1985; Lebel et al. 2001; Lebel and Trinkaus 2002).

In addition to trauma, Neanderthal remains show elevated developmental stress (Molnar and Molnar 1985; Ogilvie et al. 1989; Jelinek 1994; Berger and Trinkaus 1995). However, the degree to which this differs from stress levels in recent foraging groups is debated (Hutchinson et al. 1997; Guattelli-Steinberg et al. 2004).

Neanderthal Genetics

Neanderthals are the first extinct human species to yield genetic information. The first glimpse of their mitochondrial DNA came with the publication of the seminal article by Krings et al. (1997). These researchers were able to recover mtDNA from the Neanderthal (Feldhofer 1) type specimen and to compare it to the homologous sequence from diverse modern human populations. The Neanderthal sequence was outside the range of modern human variation and was equally dissimilar to modern human sequences from different geographic regions. It pointed to a last common ancestor for the mitochondrial genome of Neanderthals and modern humans at approximately 500 Ka (between 317 and 741 Ka).

mtDNA has now been sequenced partially or in whole for several Neanderthal specimens from diverse geographic origin (Krings et al. 1997, 2000; Ovchinnikov et al. 2000; Schmitz et al. 2002; Serre et al. 2004; Beauval et al. 2005; Lalueza-Fox et al. 2005, 2006; Caramelli et al. 2006; Orlando et al. 2006; Krause et al. 2007a; Green et al. 2008). All have yielded similar, Neanderthal-like sequences, which group together as a distinct clade, albeit with some geographic patterning (Fabre et al. 2009). On the other hand, all of the earliest Eurasian modern human specimens so far tested have yielded only modern humanlike and no Neanderthal-like mtDNA sequences (Caramelli et al. 2003; Serre et al. 2004; Krause et al. 2010; Fu et al. 2013). A recent analysis of five Neanderthal mtDNA genomes estimated the date of divergence of the Neanderthal and modern human ancestral populations in the mid-Middle Pleistocene (starting at ca. 410–440 Ka BP; Endicott et al. 2010).

More recently it has been possible to investigate also the nuclear DNA of Neanderthals. Nuclear DNA analysis has shown that Neanderthals share with modern humans the FOXP2 gene variant, one of the genes affecting language abilities, which was previously thought to be unique to modern humans (Enard et al. 2002; Krause et al. 2007a). Analysis of the nuclear DNA of an Italian Neanderthal showed that at least that individual did not share the derived allele for microcephalin with modern humans, a gene previously suggested to derive from Neanderthal ancestry (Lari et al. 2010). Ancient DNA analysis has also offered a glimpse of what Neanderthals may have looked like in the flesh: pale skin and red hair have been suggested for two Neanderthal specimens from Italy and Spain on the basis of their melanocortin 1 receptor variant (Lalueza-Fox et al. 2007). A subsequent analysis of the published genomic data from three Neanderthal individuals from Vindija, Croatia, however, indicated that they carried alleles consistent with darker skin and eyes and brown or red hair color (Cerqueira et al. 2012). These results suggest that phenotypic variability was likely high among Neanderthals.

The sequencing of the Neanderthal genome has also indicated a limited contribution [1–4 % (Green et al. 2010), recently reestimated to 1.5–2.1 % (Prüfer et al. 2014)] of Neanderthals to modern people from Eurasia. Admixture is thought to have likely occurred in the Near East and before the spread of early modern humans into the rest of Eurasia (Green et al. 2010), although other models have also been proposed (e.g., Currat and Excoffier 2011), in part to account for the observed higher admixture levels in Asia compared to Europe (Sankararaman et al. 2014; Vernot and Akey 2014). By measuring the extent of linkage disequilibrium among modern European genomes, Sankararaman et al. (2012) dated the last interbreeding between Neanderthals and modern Europeans to between 37,000 and 86,000 years BP and likely between 47,000 and 65,000. There is still discussion on whether the observed similarities can be at least in part explained by population substructure of the ancestral modern human population rather than by admixture (Eriksson and Manica 2012; Lowery et al. 2013). Nevertheless, it has been argued that such archaic interbreeding had important health consequences for modern humans (Abi-Rached et al. 2011; Sankararaman et al. 2014; The Sigma Type Diabetes Consortium in press). Some of the identified Neanderthal-derived alleles are connected with modern diseases, such as diabetes, lupus, Crohn's disease, and other conditions (Sankararaman et al. 2014). Others, however, mainly alleles relating to skin and hair, appear to have been selected for in modern humans and therefore likely provided some evolutionary advantage (Sankararaman et al. 2014; Vernot and Akey 2014). Strikingly, the modern human genome is depleted from Neanderthal-derived alleles in the X chromosomes and in genes that are expressed in the testes (Sankararaman et al. 2014). This evidence strongly suggests male infertility for Neanderthal-modern human hybrids and indicates a high level of genetic incompatibility among the two sister taxa (Sankararaman et al. 2014; Vernot and Akey 2014). This finding is compatible with the high level of morphological differentiation between Neanderthals and modern humans and accounts for the very low observed levels of admixture.

One of the unexpected results of the Neanderthal genome project has been the genetic identification of a hitherto unknown hominin lineage, dubbed the Denisovans (Krause et al. 2007b; Reich et al. 2010), first recognized through the mtDNA analysis of a phalanx from Denisova cave, in the Altai Mountains, Siberia, dating to ca. 50–30 Ka BP. The mtDNA retrieved differs from that of either modern humans or Neanderthals, and appears to belong to a hominin that shared a common mtDNA ancestor with both groups at ca. 1 Ma BP (Krause et al. 2007b). Reich et al. (2010) were able to retrieve nuclear DNA from the same bone, as well as to identify another fossil carrying the same mtDNA type. The genomic analysis showed that, contrary to the mtDNA results, the Denisovan individual likely represents a sister taxon to Neanderthals. Unlike Neanderthals, Denisovans seem to not have contributed genetically to all Eurasians, but instead to have admixed with modern Melanesian populations, which show Denisovan contribution of 4–6 % to their genetic material. On the basis of these results, it was suggested that this taxon was very widespread in Asia during the Late Pleistocene (Reich et al. 2010).

There is little understanding of what fossil taxon may correspond to the genetically identified Denisovans. A tooth from the same cave yielded the same type of mtDNA, providing a narrow glimpse on the morphology associated with this lineage (Reich et al. 2010). This specimen is a very large upper molar, likely a third molar or possibly second molar. If considered a third molar, this specimen is outside the range of variation in its crown dimensions of any taxa of the genus *Homo*, except *H. habilis* and *H. rudolfensis*. If considered a second molar, its dimensions also overlap with those of *H. erectus*. The specimen does not present any derived Neanderthal or modern human features. This question has become even more complicated by the recent discovery of Denisovan-like mtDNA in the Sima de los Huesos material (Meyer et al. 2014). These findings suggest that the Sima population may have been related to the ancestors of both Neanderthals and Denisovans or, alternatively, that gene flow between these two lineages contributed the Denisovan-like DNA to the Sima group.

Behavior

Technology

Neanderthals are most commonly, though not exclusively, associated with the Mousterian lithic technology, named after the site of Le Moustier in the Dordogne, France. Typical of Mousterian industries was the use of both Levallois and discoidal flaking techniques for the production of flakes that could be converted to a wide range of shapes, including various kinds of side scrapers, retouched points, denticulates, notches, and sometimes small handaxes (Debénath and Dibble 1994; Mellars 1996; Shea and Brooks 2000). In addition to Europe, the Mousterian is found in the Caucasus, the Near East (where it is associated with both Neanderthals and early modern humans) and North Africa (where it is not associated with Neanderthals). Mousterian industries appear in Europe as early as ~200–150 Ka and possibly earlier in the Near East, but most sites are dated to the interval from ~130 to 30 Ka.

The lithic raw material used for the production of tools in most Mousterian sites tends to be locally available. Most raw materials derive from within a 5–6 km range, and only a very small component derives from distant sources (Mellars 1996). These are mostly transported as finished tools. There is a lack of specialized use of different types of raw materials in the Mousterian, as well as a lack of specialized quarries. Very few bone tools are known (but see Soressi et al. 2013). Some points appear to have been hafted and were probably used as spear points

(Mellars 1996; Shea and Brooks 2000). Wooden tools were probably also made, as is evidenced by several well-preserved wooden spears discovered in Schöningen and dated to approximately 400 Ka (Thieme 2000) and by parts of similar implements from Clacton-on-Sea (possibly ca. 350 Ka) and Lehringen (ca. 130–110 Ka; Mellars 1996).

Neanderthal sites show relatively little structure compared to later Upper Paleolithic sites. The living areas are small and exhibit no clear focus of activity. Artificial structures are rare, although exceptions are known. Hearths are well defined and were probably central in tool production and bone processing but are not consistent in their location (Mellars 1996). Controlled use of fire appears widespread in Europe from the Middle Pleistocene Oxygen Isotope Stage (OIS) 11 (~400 Ka) onward and possibly earlier (Gowlett 2006).

Until recent years, the Mousterian was commonly thought to represent a static culture. However, redating of Mousterian sites has shown changes with time in regional industries from Europe and the Near East (Shea and Brooks 2000). Additionally, reanalysis of some Mousterian sites has shown technological responses to climatic changes (Kuhn 1995; Shea and Brooks 2000). Some "transitional" Middle-Upper Paleolithic industries, like the Châtelperronian industry in France, the Uluzzian in Italy, and the Szeletian in East-Central Europe, also show strong affinities with the Mousterian. These were originally thought to have been made by early modern humans, also generally considered responsible for the Aurignacian industry. Since the Châtelperronian has been found associated with Neanderthal skeletal remains in two sites in France, St. Césaire, and Arcy-sur-Cure (Lévêque and Vandermeersch 1980; Hublin et al. 1996), it has been widely held that at least some of these transitional industries were produced by late Neanderthal populations. This in turn has prompted intense debate over the identity of the makers of these industries, the possibility of Neanderthal acculturation by, or trade with, early modern humans, and the cognitive capacities and ability for symbolic thought in Neanderthals (d'Errico et al. 1998; Zilhão and d'Errico 1999; Mellars 1999, 2005; Klein 2000; Harvati et al. 2003; Bar-Yosef 2005; Gravina et al. 2005; Svoboda 2005; Hublin et al. 2012). Recently Benazzi et al. (2011) identified the only known human remains associated with the Uluzzian (two milk molars from Grotta del Cavallo, Italy) as representing modern human, rather than Neanderthal, children. These remains furthermore represent the earliest known modern human remains in Europe (dated to between ca. 42 and 45 Ka calibrated BP through AMS ^{14}C dating on shell). This discovery suggests that at least the Uluzzian was produced by modern humans and further complicates our understanding of the transitional industries in Europe.

Subsistence

Neanderthal sites abound in faunal remains of various taxa, indicating a high reliance on meat in their diet. Large palearctic mammals are most commonly found in these assemblages, including bison, wild cattle, horse, reindeer, red and fallow deer, ibex, wild boar, and gazelle (Shea and Brooks 2000). Sites from the high latitudes of Northern and Central Europe indicate an almost exclusive reliance on large- to medium-sized mammals, with very little small game and low diversity of animals consumed (e.g., very few bird or fish remains; Hockett and Haws 2005). Middle-latitude Neanderthal sites (Southwestern France and Northern Spain) also show low diversity and a focus on terrestrial mammals but indicate a somewhat greater reliance on medium-sized mammals. Sites from the Mediterranean region still show reliance on large- and medium-sized terrestrial mammals but also preserve evidence for consumption of other food sources, such as shellfish, birds, tortoises, and marine mammals (Stiner 1994; Barton 2000; Currant 2000; Hockett and Haws 2005; Stringer et al. 2008; Harvati et al. 2013). Plant remains in Neanderthal sites are rare, likely due to their poor preservation. Phytoliths and other vegetal remains known primarily from Mediterranean sites point to a plant component in Neanderthal diet which probably included wild legumes and grasses as well as seeds and fruit (e.g., Gale and Carruthers 2000; Madella et al. 2002; Lev et al. 2005). Recent work on dental calculus recovered from Neanderthal teeth has confirmed such strong plant components in Neanderthal diets and has also pointed to cooking and potentially medicinal use of plants (Henry et al. 2011; Hardy et al. 2012).

In addition to direct evidence of faunal and plant remains from archaeological sites, Neanderthal diets can be assessed using the isotopic signature of the Neanderthal skeletons themselves. Analysis of the stable isotopes of carbon and nitrogen has now been undertaken for a number of Neanderthal specimens from a wide time range (~130–30 Ka) and so far has invariably indicated a very strong reliance on herbivore meat (Fizet et al. 1995; Bocherens et al. 1999, 2005; Richards et al. 2000). All Neanderthal bones so far analyzed are similar to top predators in their isotopic composition. Furthermore, some of the isotopic studies suggest a much greater reliance on very large herbivores, such as wholly rhinoceros or wholly mammoth, than had been previously thought based on the faunal archaeological evidence (Bocherens et al. 2005). The isotopic analyses agree with zooarchaeological studies in suggesting a very small component of marine foods in Neanderthal diets, in sharp contrast with later, Upper Paleolithic modern humans (Richards et al. 2001, 2005).

The degree to which Neanderthals obtained meat through hunting as opposed to scavenging has been a subject of debate (Binford 1983; Chase 1986; Stiner 1990). Some have suggested that the relative significance of these two activities probably varied seasonally and from region to region (Shea and Brooks 2000). Among the arguments brought forth to support scavenging as the primary Neanderthal activity is the high proportion of cranial faunal remains in Neanderthal sites and the age profile of the remains, thought to be for the most part old individuals rather than prime-age adults (Binford 1983). However, a bias toward cranial remains may simply represent a bias in the butchering and transportation of large carcasses (Mellars 1996). The age-mortality profile is now known to vary, with several French Middle Paleolithic sites showing a catastrophic mortality profile inconsistent with hypotheses of scavenging (summarized in Mellars 1996).

Further evidence in support of hunting comes from the wooden spears from Schöningen dated to 400 Ka (Thieme 2000), although there is disagreement as to whether these represent throwing or thrusting spears. Finally, the Neanderthal stable isotopic signature suggests active predation on the part of the Neanderthals and is difficult to reconcile with a subsistence strategy consisting primarily of scavenging (Richards et al. 2000).

Symbolic Thought and Language

The Neanderthal ability for symbolic thought and language is hotly debated. The archaeological record shows a dearth of "symbolic" objects, such as objects of art or personal ornamentation, in Mousterian assemblages, compared not only with later Upper Paleolithic industries (Mellars 1996) but also with some penecontemporaneous African sites (McBrearty and Brooks 2000; Henshilwood et al. 2001; but see Zilhão et al. 2010; Peresani et al. 2011). The relative scarcity of such objects has been argued to indicate a lack of human cognitive abilities and language. However, it has also been pointed out that the archaeological record is a very limited and imperfect record of behavior, perhaps in this case resulting in a biased documentation (or lack thereof) of Neanderthal symbolic activities. The discovery of Neanderthal remains associated with transitional industries, and, in the case of Arcy-sur-Cure, with lavish personal ornaments, has raised tremendous discussion over the identity of the makers of these objects, as well as the processes that would have led to their association with Neanderthals (i.e., trade, acculturation, or endogenous development; see, e.g., Hublin et al. 1996, 2012; d'Errico et al. 1998; Zilhão and d'Errico 1999; Mellars 1999, 2005; Klein 2000; Harvati et al. 2003; Bar-Yosef 2005; Benazzi et al. 2011).

Evidence in support for Neanderthal ability for some symbolic thought is the occurrence of ochre and manganese "crayons" in Neanderthal sites and the burial of at least some Neanderthal skeletal remains. Although the apparent Neanderthal burials have been argued to be simply the product of natural processes (Gargett 1999), the recovery of a number of largely complete skeletons from diverse sites found in articulation and placed in shallow pits is strongly indicative of intentional burial. Nevertheless, evidence for grave goods and other burial practices is scant and controversial (Mellars 1996; Shea and Brooks 2000).

In terms of the anatomical evidence for language and cognition, Neanderthals possessed cranial capacities as large as or larger than modern humans. Their endocasts show similar features to those of modern humans and similar left-right asymmetries (Holloway 1985) although they retain an "archaic" overall shape (Bruner et al. 2004; see also Gunz et al. 2010; Bastir et al. 2011). The relatively flat Neanderthal cranial base was long considered to indicate a larynx positioned so high that it would preclude the production of certain speech sounds and particularly of vowels crucial to speech perception (Lieberman and Crelin 1971; Laitman and Heimbuch 1982; Lieberman 1989). This hypothesis was most recently tested by Barney et al. (2012) who used extensive modern human reference series and a large number of fossils to reconstruct the Neanderthal vocal tract and to simulate its articulatory potential. This study found that, although Neanderthals probably had a limited production of vowels compared to modern humans, this limitation would likely not have affected the/i/and/u/vowels that are critical for speech. A further attempt to infer language capabilities from the bony morphology focused on the hypoglossal canal, which transmits the nerves to the exceptionally large human tongue musculature. The size of the hypoglossal canal was found to be similar in Neanderthals and modern humans and larger than in earlier hominins (Kay et al. 1998), suggesting a similar function for the Neanderthal tongue in speech production. More recent work, however, has questioned this evidence (DeGusta et al. 1999). Neanderthals are also similar to modern humans and unlike earlier hominins in their enlarged thoracic vertebral canals, which could indicate an expansion of thoracic innervation (MacLarnon and Hewitt 1999). The resulting greater control of the intercostal musculature would enhance breathing control and could indicate the ability for speech. Finally, the anatomy of the outer and middle ear in the Middle Pleistocene pre-Neanderthal fossils from Sima de los Huesos (Atapuerca, Spain) was found to be similar to that of modern humans and specialized for speech perception (Martínez et al. 2004), supporting speech capabilities for Neanderthals and their ancestors.

Evolution and Classification

The “Accretion Hypothesis”

The “Accretion Model” for the evolution of Neanderthals (Dean et al. 1998; Hublin 1998) accounts for the progressive appearance of Neanderthal morphology through time, beginning around 450 Ka (OIS 12). According to this hypothesis, the Neanderthal lineage became isolated in Europe due to the severe glacial conditions prevailing in the Balkans at this time, in combination with enlarged Caspian and Black seas and increased aridity in North Africa and the Levant (Stringer 2012). In these conditions of isolation, the Neanderthal morphology is thought to have become gradually fixed, partly through natural selection as an adaptation to cold-climate conditions but perhaps primarily through the process of genetic drift (Hublin 1998; Stewart and Stringer 2012).

Although the accretion process of Neanderthal features is mosaic in nature, facial and mandibular features have been argued to be established first, followed by features in the occipital region and finally in the temporal bone and vault (Dean et al. 1998; Hublin 1998; Rightmire 1998). This pattern, however, is complicated by uncertainties in the chronology of the skeletal material (especially the very old ages proposed for the Sima de los Huesos remains; see Stringer 2012) and in the polarity of some of the relevant features (see Harvati et al. 2010; Freidline et al. 2012). Four broad stages of Neanderthal evolution have been described (Dean et al. 1998; Hublin 1998). Stage 1 includes “early pre-Neanderthals,” i.e., the Middle Pleistocene archaic specimens, such as Petralona, Arago, and Mauer, dating from before

OIS 12. These hominins are considered to show incipient Neanderthal features mainly in the facial region (although some of these features may represent primitive retentions; Harvati et al. 2010). They also show strong similarities with African and Asian contemporaries (e.g., Stringer 1974; Mounier et al. 2009; Harvati et al. 2010; Schwartz and Tattersall 2010). Stage 2 (OIS 11-9) specimens are termed "pre-Neanderthals" (e.g., Steinheim, Swanscombe). They are thought to exhibit Neanderthal morphology more clearly, showing Neanderthal features also in the occipital area. Stage 3 (OIS 7-5, Biache, Krapina, Saccopastore) "early Neanderthal" specimens show most Neanderthal traits in the posterior cranium and some also in the temporal region. Finally, Stage 4 comprises the "classic Neanderthals" of OIS 4 and 3 (Neanderthal, La Chapelle-aux-Saints, Amud), showing fully expressed Neanderthal morphology.

Classification of Middle Pleistocene Humans

According to the accretion hypothesis, Neanderthal evolution was an anagenetic process with no speciation event resulting in the appearance of this taxon. Within the framework of this model, Neanderthals can be viewed either as a subspecies of *H. sapiens* or as a full, distinct species, *H. neanderthalensis*. If the latter classification is accepted, then the position of the Middle Pleistocene specimens from Europe must be clarified. Traditionally, these have been included in the species *H. heidelbergensis* in which African Middle Pleistocene humans have also been placed, due to extensive observed morphological similarities between the European and African Middle Pleistocene human fossils (e.g., Stringer 1974, 1984; Arsuaga et al. 1997; Rightmire 1998, 2007, 2008; Harvati 2009; Mounier et al. 2009; Harvati et al. 2010). This taxon is viewed by some as ancestral to both Neanderthals and modern humans (e.g., Rightmire 1998, 2008, 2009; Stringer 2012). If the European *H. heidelbergensis* was exclusively ancestral to Neanderthals, this sample could be placed within the Neanderthal lineage and within the taxon *H. neanderthalensis* (e.g., Stringer 1995, 2012; Hublin 1998, 2009). Alternatively, the European lineage could be arbitrarily split into two paleospecies, the earlier segment retaining the nomen *H. heidelbergensis* and the later *H. neanderthalensis* (e.g., Arsuaga et al. 1997; Manzi 2004; but see Wolpoff et al. 1994; Rosas et al. 2006; Tattersall and Schwartz 2006; Bräuer 2008). In either case, the African Middle Pleistocene specimens would have to be placed into another taxon, possibly *H. rhodesiensis* or *H. helmei* (Stringer 1995, 2012). The position of the Sima de los Huesos in this scheme is crucial, as these specimens exhibit very strong Neanderthal similarities (e.g., Rak et al. 2011; Gomez-Robles et al. 2012; Martinón-Torres et al. 2012) while argued to be >530 Ka old (Bischoff et al. 2007), thus providing a very strong link between European *H. heidelbergensis* and later Neanderthals. Recently Stringer (2012) questioned this age estimate due to taphonomic considerations and proposed that the Sima de los Huesos specimens can be considered early Neanderthals instead of *H. heidelbergensis*.

Neanderthal Taxonomy and the Neanderthal Role in Modern Human Evolution

Ever since their assignment to the distinct species *Homo neanderthalensis* (King 1864), the classification of Neanderthals and their role in human evolution have been the subject of intense discussion. Current consensus sees Neanderthals and earlier Middle Pleistocene European extinct humans as a separate evolutionary lineage, at least partly geographically isolated in Western Eurasia. What is still unclear, however, is the nature of the interaction between Neanderthals and modern humans arriving in Europe ca. 45 Ka BP (Benazzi et al. 2011; Higham et al. 2011a, b). Since the two taxa likely overlapped in Europe for some millennia, it is widely thought that they would have met at least on some occasions (although the duration of their coexistence is debated, as is contact between them; e.g., Finlayson 2004; Pinhasi et al. 2011, 2012). The nature of their interaction and the possibility and extent of interbreeding during these encounters are central points of discussion.

Although there is no doubt that Neanderthals were our closest relatives, the magnitude of anatomical differences between Neanderthals and modern humans is such that several authors recognize the former as a distinct species under species definitions that use morphological criteria (e.g., Stringer 1974; Tattersall 1992; Stringer and Andrews 1988; Hublin 1998; Harvati 2003b; Harvati et al. 2004). The long list of uniquely derived Neanderthal features, many of which appear early in ontogeny (e.g., Maureille and Bar 1999; Ponce de León and Zollikofer 2001), points to distinct species status under the phylogenetic species concept (e.g., Hublin 1978; Santa Luca 1978; Stringer et al. 1984; Tattersall 1986, 1992, 2000; Stringer and Andrews 1988; Schwartz and Tattersall 1996a, b). Furthermore, the cranial morphological distance between Neanderthals and modern humans is more similar to interspecific than to intraspecific distances observed among primate species and their subspecies, suggesting a distinct species status as appropriate for Neanderthals (Harvati 2003a; Harvati et al. 2004).

Some paleoanthropologists see evidence for admixture in the fossil record and have therefore argued for subspecific status for Neanderthals following the biological species concept. These authors have pointed out Neanderthal-like features in early modern European specimens and trends of morphological "modernization" in some late Neanderthal samples, as well as proposed individual specimens as potential hybrids (e.g., Smith 1982, 1992; Wolpoff 1989; Frayer 1992; Frayer et al. 1993; Duarte et al. 1999; Ahern et al. 2002; Trinkaus et al. 2003; Soficaru et al. 2007). However, others have rejected these claims (e.g., Lahr 1996; Bräuer and Broeg 1998; Tattersall and Schwartz 1999; Bräuer et al. 2004, 2006; Bailey 2002; Harvati 2003a, 2009; Harvati et al. 2004, 2007).

From a genetic perspective, the mtDNA of Neanderthals and Upper Paleolithic Europeans shows no evidence for admixture between the two groups (Wolpoff et al. 2001; Serre et al. 2004; Green et al. 2008), although demographic modeling indicates that a small contribution of Neanderthals to the modern human gene pool is consistent with this result (<1–2 %; Currat and Excoffier 2004; Weaver and Roseman 2005). The recent publication of Neanderthal genomic data, however (Green et al. 2010; Prüfer et al. 2014), showed the Neanderthal genome was more similar to that of Eurasians than Africans. This evidence suggests that limited interbreeding may have occurred during the earliest dispersal of modern humans out of Africa. Green et al. (2010) estimated the proportion of Neanderthal-derived DNA in modern Eurasians to be ca. 1–4 %. This estimate was further refined to 1.5–2.1 % by Prüfer et al. (2014). Demographic modeling of admixture combined with territorial expansion under this level of introgression has pointed to very low (<2 %) interbreeding rates and was interpreted as showing strong reproductive barriers between Neanderthals and modern humans (Currat and Excoffier 2011). Nonetheless, discussion is ongoing on whether population substructure in ancestral modern humans can also account for at least part of the observed patterns (Eriksson and Manica 2012; Lowery et al. 2013).

The inability to reproduce successfully is the criterion for species recognition under the commonly applied biological species concept. Nonetheless, closely related mammal species, including primates (see Jolly 2009), are known to hybridize. (Indeed recent genetic evidence indicates that such interbreeding may have been the case among several hominin species: Denisovan DNA was found at frequencies up to 6 % in modern Melanesians, suggesting an admixture event between modern humans and this extinct taxon (Reich et al. 2010), and archaic admixture has been proposed for some Central African modern human populations (Hammer et al. 2011; see also Harvati et al. 2011). Furthermore, interbreeding has been suggested between Neanderthals and Denisovans, as well as between the latter and an unknown, older species, possibly *Homo erectus* (Prüfer et al. 2014). Therefore, a low level of interbreeding between Neanderthals and modern humans is not necessarily inconsistent with a separate species assignment of Neanderthals (see Hofreiter 2011; Stringer 2012). This is especially true if there was strong reproductive isolation between the two taxa, possibly related to reduced hybrid fitness, as suggested by Currat and Excoffier (2011). Recent genomic analysis in modern humans showed that entire genome regions are depleted of Neanderthal-derived alleles, including most importantly the X chromosome and genes expressed in the testes (Sankararaman et al. 2014). This pattern is consistent with male hybrid sterility and strongly suggests post-zygotic isolating mechanisms between Neanderthals and modern humans. The two taxa were therefore likely largely genetically incompatible and in the process of speciation. This genomic evidence agrees with the great morphological differences described between the two taxa. It also accounts for the very low interbreeding rates observed, as well as for the ambiguous evidence for admixture in the fossil record. Partial reproductive isolation, if supported by future analyses, would also be consistent with the recognition of Neanderthals as a distinct species under the biological species concept.

The Neanderthal Extinction

The last appearance date of Neanderthals is not well dated. The most recent radiometric evidence points to their disappearance around or soon after 40 calendar Ka BP (e.g., Pinhasi et al. 2012; Wood et al. 2013) and to the first appearance of modern humans in Europe as early as approximately 45 calendar Ka BP (Benazzi et al. 2011; Higham et al. 2011a, b). These results suggest that Neanderthals and early modern humans probably overlapped in Europe for some millennia (e.g., Pinhasi et al. 2012). For some researchers, the last appearance of Neanderthals simply signifies their assimilation into the modern human gene pool (Smith et al. 2005; Svoboda 2005). Although genomic research is ongoing, the evidence recovered as yet suggests minimal admixture on the order of 1.5–2.1 % (Prüfer et al. 2014), which is likely not compatible with a full assimilation scenario. Most researchers view the Neanderthal demise as a true extinction, even if limited genetic exchanges with modern humans took place.

Several scenarios for the Neanderthal extinction have been proposed, and often they invoke some direct or indirect competition with early modern humans arriving in Europe shortly before Neanderthals disappear. Proposed modern human competitive advantages range from demographic factors, such as small differences in birth and mortality rates or in interbirth spacing (Zubrow 1989; Skinner 1997; Flores 1998), to larger group sizes and higher population density among Upper Paleolithic modern humans (Gat 1999; Mellars and French 2011), to greater dietary diversity in Upper Paleolithic modern humans (Richards et al. 2001; Hockett and Haws 2005). The role of climate was until recently not emphasized, as Neanderthals disappeared in OIS 3, during what was thought to be relatively stable conditions preceding the last glacial maximum (Stringer et al. 2003). Some recent hypotheses, however, consider climatic and environmental factors to be major driving forces. It has been proposed that habitat degradation and fragmentation led to the disappearance of Neanderthal populations, with modern humans arriving in areas previously occupied by Neanderthals after the latter were already extinct (Finlayson 2004). The Neanderthal demise has also been viewed as one of the many Late Pleistocene megafauna extinctions caused by the loss of an environment with no modern analogue (Stewart et al. 2003; Stewart 2005).

Available paleoclimatic records have shown that OIS 3 was dominated by much more unstable climatic conditions than previously thought, possibly precipitated by unusually intense volcanic activity (Golovanova et al. 2010), leading to a reexamination of the role of climate deterioration in the Neanderthal demise (van Andel and Davies 2003; but see Lowe et al. 2012). The argument has also been made that no two cooling episodes are the same and that taxa surviving one cooling episode may not persist through the next (Stewart 2005). An alternative interpretation, however, sees the advent of modern humans, perhaps with better cultural buffeting and more effective social networks, as providing the *coup de grâce* to the highly stressed Neanderthal populations through competition for severely limited resources during the critical time interval of their coexistence in Europe (Stringer et al. 2003; see also Lahr and Foley 2003). In this view, it is the interaction between the effects of fluctuating climate and environment and of competition with modern humans that led to the eventual Neanderthal extinction.

Conclusions

The most striking advances in Neanderthal research since the publication of the first edition of this volume come undoubtedly from the realm of ancient DNA. In the last few years, aDNA analyses, and particularly genomic analyses, have made it possible to gain insight on diverse aspects of Neanderthal paleobiology, from their phenotypic appearance to their population structure. They have also shed light on the genetic interactions between Neanderthals and modern humans, as well as, most recently, on the evolutionary advantages and disadvantages that such genetic interactions conferred to our ancestors. Methodological advances have now made it possible to recover DNA from even more ancient remains, as evidenced by the recently published mtDNA from the Sima de los Huesos, renewing hope that other limitations may be overcome in the future. A major achievement would be the retrieval of aDNA from early modern human fossils from the Near East and Africa.

A second set of methodological advances has come from the realm of dating, particularly the dating of the late Neanderthal and early modern European sites. Refinements in radiocarbon dating, as well as the implementation of the dating of volcanically derived sediments, have made a major impact in our understanding of the chronology of coexistence, which provides the framework for Neanderthal-modern human interactions and for the Neanderthal extinction. Ongoing paleoclimatic analyses will help pinpoint the still unresolved role of changing environmental conditions in these processes. Finally, the advent of powerful imaging and morphological analysis of fossils has enabled the retrieval of crucial information even from fragmentary and previously uninformative specimens, in some cases overturning previous hypotheses, as well as further illuminated the paleobiology of Neanderthals and our own ancestors. The combined efforts of these approaches promise an exciting era of breakthroughs in the coming years.

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Homo floresiensis

Leslie C. Aiello

Contents

Abstract

Homo floresiensis was announced in 2004 as a new, late surviving hominin species that lived between ~74 and 17 ka on the Indonesian island of Flores. Since then, there has been considerable controversy over its evolutionary position. *H. floresiensis* is a small-bodied and small-brained hominin that has a unique mosaic morphology which, taken at face value, suggests that its closest evolutionary affinity is with early *Homo*. Various analyses have suggested either *H. habilis*, *H. georgicus*, or *H. erectus* from Africa or Asia as the most probable ancestor. The alternative to this "new species" hypothesis is that *H. floresiensis*, and particularly the LB1-type skeleton, represents a pathological modern human suffering from one or a combination of syndromes, which produce disordered growth (dwarfism) and microcephaly. Both hypotheses have compelling aspects, but the "pathological modern human" hypothesis has yet to account for the total

L.C. Aiello (✉)
Wenner-Gren Foundation, New York, NY, USA
e-mail: laiello@wennergren.org

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morphological pattern observed in *H. floresiensis*. At present this is a less convincing hypothesis than the "new species" hypothesis. Recent research is pointing to a *H. erectus* as the most plausible *H. floresiensis* ancestor. It is known from Island Southeast Asia in the proper time frame and would avoid the paradigm changing necessity of postulating an unknown Asian pre-*erectus* ancestor. However, many questions remain and the issues surrounding *H. floresiensis* will not be resolved without further analysis and discovery.

Introduction

Homo floresiensis is a hominin taxon erected by Brown et al. (2004) on the basis of a partial skeleton (LB1) (holotype) and a single tooth (LB2) (paratype) discovered in 2003 at the cave site of Liang Bua on the island of Flores, Indonesia (Figs. 1 and 2). Further hominin material was recovered in 2004 (Morwood et al. 2005), and the hypodigm now includes over 100 numbered specimens representing 9–14 individuals (Morwood et al. 2005, 2009). The majority of the material, including the LB1-type skeleton, dates between ~18 and 16 ka and was found by the east wall of the cave (Morwood et al. 2004; Roberts et al. 2009; Westaway et al. 2009a). Other material dates between ~74 and 61 ka and is located near the west wall in the center of the cave.

The hominin remains are variously associated with stone tools that have been described as relatively advanced. They are also variously associated with a dwarfed

Fig. 1 The Liang Bua cave (2007) (Photo: Djuna Ivereigh/ARKENAS)

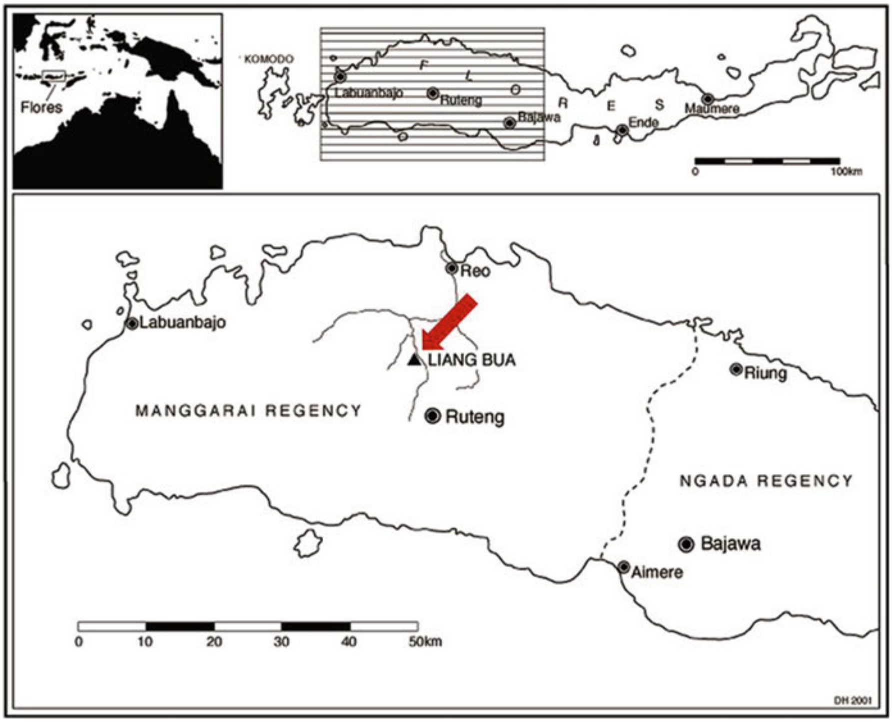

Fig. 2 Map of island Southeast Asia showing the location of Flores and Liang Bua (Map credit: Mike Morwood, modified from Aiello 2010)

species of *Stegodon* (*Stegodon florensis insularis*), the only other large mammal on the island; the Komodo dragon; giant rats; bats; and birds including the giant, 1.8 m tall, carnivorous marabou stork, *Leptoptilos* sp. (Van den Bergh et al. 2009). Some of *Stegodon* bones show cut marks (Morwood et al. 2005). The LB1-type skeleton was found in a situation suggesting that it was rapidly covered in a standing pool of water. Other *H. floresiensis* material was found in association with charred bone and reddened fire-cracked rocks suggesting the use of fire. There is no evidence of high-level cognition such as the burials, personal ornamentation, or ocher found with contemporaneous hominins elsewhere in the world.

General Description

The material represents individuals that were relatively small in stature. The LB1-type skeleton (Fig. 3) has been estimated to have stood ~106 cm tall (Brown et al. 2004), and the other adult material has been estimated to have been smaller. There is only one known cranium (LB1), and this has a cranial capacity of 380–426 cm^3, with 426 cm^3 being the most recent and accurately determined estimate (Brown et al. 2004;

Fig. 3 The LB1 *Homo floresiensis* skeleton (Photo: Bill Jungers)

Falk et al. 2005a; Holloway et al. 2006; Kubo et al. 2013). The *H. floresiensis* cranium is reminiscent of *Homo erectus* (Brown et al. 2004; Baab and McNulty 2009; Baab et al. 2013) (Fig. 4), while the LB1 skeleton has limb proportions that resemble *Au. afarensis* with short legs relative to arms and other postcranial features that individually are most similar either to apes, to australopithecines, or to *Homo erectus* or are totally unique such as its unusually large feet (Jungers et al. 2008, 2009a).

The Context of *Homo floresiensis*

Current evidence suggests that *H. floresiensis* spans the period from ~74 to ~17 ka, and during this time, the environment around the Liang Bua cave fluctuated from humid forest to grassland, influenced by the glacial phases (Westaway et al., 2009b). The uppermost *H. floresiensis* deposits are capped by volcanic layer reflecting a massive eruption, although it is unclear whether the disappearance of *H. floresiensis* was directly related to this eruption or was related to climate change,

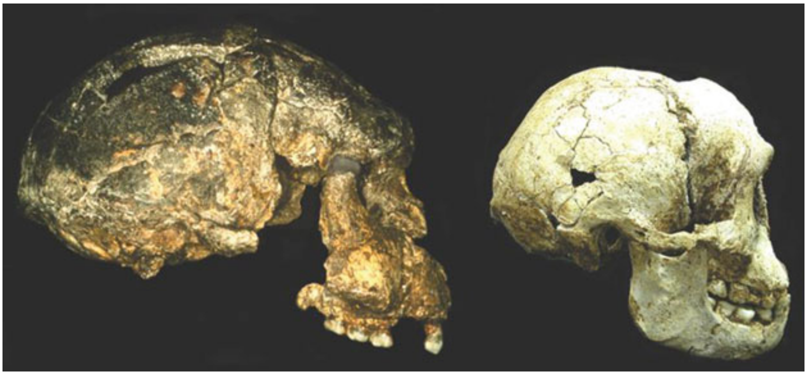

Fig. 4 Javanese *Homo erectus* (Sangiran 17) (*left*) and *Homo floresiensis* (LB1) (*right*) (Photo: Peter Brown)

to the arrival of modern *H. sapiens*, or to a combination of events (Morwood et al. 2009). Modern humans and their cultural remains are found in higher levels of Liang Bua, dating to ~11 ka (see Moore et al. 2009).

There is evidence from stone tools that there were hominins in the vicinity of the cave at the earlier period of ~190 ka (Westaway et al. 2009a, b). Elsewhere on Flores in the Soa Basin, there is archaeological evidence that hominins were present at other sites such as Mata Menge at 800–880 ka (Morwood et al. 1998; Brumm et al. 2006; Moore and Brumm 2007) and at Wolo Sege at 1.02 ± 0.02 Ma (Brumm et al. 2010). It is unknown who these hominins were, and it is possible that hominin occupation on Flores predates the oldest Soa Basin deposits.

What Is *Homo floresiensis*?

There are two competing hypotheses to explain the existence of *H. floresiensis*. The first is supported by the discovery team as well as many other paleoanthropologists and posits that *H. floresiensis* represents a new species of hominin that survived into relatively recent times in an island refugium environment (e.g., Argue et al. 2006, 2007, 2009; Brumm et al. 2006; Falk et al. 2005a, b, 2006, 2007a, b, c; Larson 2007; Larson et al. 2007a, b; Tocheri et al. 2007; Zeitoun et al. 2007; Van Heteren and de Vos 2007; Morwood and van Oosterzee 2007; Gordon et al. 2008; Jungers et al. 2008, 2009a; Lyras et al. 2009; see also Morwood and Jungers 2009a and the papers therein). The original interpretation was that it represents a dwarfed island descendant of the larger-bodied *Homo erectus*, which is well known from other sites in Indonesia (e.g., Brown et al. 2004). Others suggest that it was a pre-*erectus* hominin that arrived on Flores with both a small body and a small brain (Brown and Maeda 2009; Morwood and Jungers 2009b).

The alternative major hypothesis is that the LB1 skeleton represents a modern individual suffering from one of the many syndromes which, either individually or in combination, result in microcephaly and disordered growth (e.g., Weber et al., 2005; Martin et al. 2006a, b; Martin 2007; Richards 2006; Henneberg 2007; Hershkovitz et al. 2007; Tuttle and Mirsky 2007; Henneberg and Schofield 2008; Rauch et al. 2008; Obendorf et al. 2008; Oxnard et al. 2012). The LB6 mandible, which is more recent that the LB1 skeleton, is considered to represent another afflicted individual, while the other material is too fragmentary to determine whether individuals were healthy or not. Indriati (2007) has observed that scientists with broad backgrounds dealing with modern human variation (e.g., geneticists, clinicians, and human biologists) tend to favor a pathological explanation in contrast to the paleoanthropologists who tend to favor the "new species" hypothesis.

Both major hypotheses have compelling aspects. The "new species" hypothesis in either of its variants foregrounds *H. floresiensis* cranial and postcranial anatomy, which is not known to be mimicked by the various pathological conditions put forward to support the "pathological modern human" hypothesis. However, this second hypothesis is considered by its supporters to be a more parsimonious explanation for the occurrence of *H. floresiensis*, who was living contemporaneously with anatomically modern humans in Island Southeast Asia (e.g., Oxnard et al. 2012). In addition to arguments for a number of syndromes in modern humans that can produce short stature and microcephaly, these scholars point to major questions about insular dwarfism as an explanation for the small *H. floresiensis* brain and ask whether a small-brained hominin would be capable of the level of cultural complexity suggested by the archaeological context or could have survived in a small island environment when contemporaneous modern humans are known from the area from ~50 ka (O'Connor 2007).

Morphology of *H. floresiensis*

One of the main arguments against the "new species" hypothesis for *H. floresiensis*, particularly if its antecedent was a relatively large *H. erectus*, has been that the degree of brain size reduction in *H. floresiensis* is simply too great to be explained by insular dwarfism (Martin et al. 2006a, b; Martin 2007). Dwarfed animals, including humans, generally have larger brains relatively to their body sizes (higher encephalization quotients) than their larger antecedents (Schoenemann and Allen 2006). This is because, in insular dwarfism, bodies reduce along a steeper curve than brains. But recently Kubo et al. (2013) have argued that up to 50 % of the brain size reduction in *H. floresiensis* may be explained by body size reduction alone. The remaining reduction could be accounted for by a number of factors. For example, in altricial animals, dwarfing along an ontogenetic rather than the adult allometric curve may be a more appropriate model. If this was true for *H. floresiensis*, it is conceivable that an *H. erectus* ancestor could have given rise to *H. floresiensis*, particularly if the ancestor was relatively small brained like early *H. erectus* from Java (Weston and Lister 2009; Kubo et al. 2013). Another factor may be adaptation to conditions where energetic concerns are important, and a small and energetically less expensive brain would be an advantage (Taylor and van Schaik 2007; Kubo et al. 2013; see also Köhler and Moyà-Solà 2004). However, the smaller the brain size of the ancestor, the more likely that insular dwarfism may have been a factor, and this is one reason why many paleoanthropologists favor a smaller-brained pre-*erectus* ancestor for *H. floresiensis*.

Brain shape (endocranial cast shape) has been used in support of the "new species" hypothesis (Falk et al. 2005a, 2007a, 2009b), which argues that it is different from modern microcephalic endocasts and resembles most closely *H. erectus* endocasts. However, critics point out that microcephalic endocranial casts are highly variable and that the *H. floresiensis* endocranial cast can be matched in some microcephalics (Weber et al. 2005; Martin et al. 2006a, b; Martin 2007). The most recent analysis in a long debate on this issue is based on craniometric ratios and suggests that the LB1 endocranial cast falls within the range of the microcephalics and outside the range of modern normal human and *H. erectus* endocasts (Vannucci et al. 2011). However, these authors caution that this analysis does not necessarily prove that *H. floresiensis* is a microcephalic. They call for more comprehensive 3D morphometric analyses and ideally the discovery of more fossils or DNA evidence that would definitively settle the issue one way or another.

Evidence from the cranium and mandible is less ambiguous. In the original publication, the small LB1 cranium was described as being similar in shape to *H. erectus* (Brown et al. 2004). The cranium is broad in relation to its height, and the greatest breadth is at the level of the inflated supramastoid region. Both facial height and prognathism are reduced in relation to pre-*Homo* hominins, and in lateral view the infraorbital region is oriented posteriorly. The mandible lacks a chin and has a developed alveolar planum, with a robust superior transverse torus, a deep digastric fossa, and a low, rounded inferior transverse torus.

Detailed metric analyses have confirmed similarity to early *Homo* (variously *H. habilis*, *H. georgicus*, or *H. erectus* from Africa and Asia) (Argue et al. 2006; Zeitoun et al. 2007; Gordon et al. 2008; Martinez and Hamsici 2008; Lyras et al. 2009; Baab and McNulty 2009; Baab et al. 2013). Baab et al. (2013) point out some similarity in shape between LB1 and modern human microcephalic specimens, although they emphasize that in features that distinguish microcephalics from *H. erectus*, LB1 is most similar to the fossils. They also note that because of the small size of LB1, the allometries in facial morphology converge on what has been interpreted as a more modern face (Baab and McNulty 2009). 3D morphometric analysis of the LB1 mandible also confirms morphological similarity to fossil hominins and difference from modern humans, including microcephalics (Viterbo et al. 2012).

The postcrania also has many features reminiscent of fossil hominins, particularly in the hand, foot, and shoulder (Tocheri et al. 2007, 2008; Larson 2007; Larson et al. 2007a, b, 2009; Jungers et al. 2008, 2009a, b). The wrist bones (trapezoid, scaphoid, and capitate) have a primitive morphology for the African ape-human clade, which is more primitive than the morphology represented in *H. antecessor* and the Neanderthals (Tocheri et al. 2007, 2008), although aspects of the proximal and distal pollical (thumb) phalanges are more similar to modern humans (Crevecoeur et al. 2012).

The shoulder is also primitive in form, with a short clavicle and a humerus with a low degree of torsion (Larson 2007; Larson et al. 2007a). This morphology predates *H. antecessor* and is shared with earlier hominins (early *Homo erectus* (Nariokotome) and *H. georgicus*).

The foot is also unusual in a number of features. In particular, the navicular appears to have been weight bearing, suggesting that *H. floresiensis* lacked a transverse arch. The pedal phalanges are moderately curved, resembling some australopithecines, and the forefoot is long in relation to the tarsal skeleton. The entire foot is also long in relation to the length of the femur and the tibia (Jungers et al. 2009a, b).

Other aspects of the skeleton show a mixture of features. For example, the femur resembles australopithecines in being relatively short with a small head and anteriorly-posteriorly compressed neck. However, it differs from them in having a laterally expanded greater trochanter and a well-developed intertrochanteric crest (Jungers et al. 2009b; Richmond and Jungers 2008). The pelvis is also a mosaic, with an australopithecine-like laterally flaring iliac blade and a small acetabulum. However, the acetabulum is distinguished from these earlier hominins in having a superior portion of the acetabular lunate surface that is broader than the posterior horn.

Taken together, the postcranial morphology suggests a different locomotor and manipulative functionality than found in modern humans. For example, the absence of a transverse arch in the foot and the long, moderately curved pedal phalanges suggest a non-modern pattern of weight transfer through the foot during the stance and toe-off phases of walking. The long foot would also suggest clearance problems during the swing phase, and the conclusion would be that the kinematics of both walking and running would be different from modern humans (Jungers et al. 2009a, b). This, together with the relatively short clavicle and resulting narrow upper thorax, would be inconsistent with endurance running (e.g., Bramble and Lieberman 2004), while the shoulder morphology in itself would not be compatible with modern human throwing ability (Larson 2007; Larson et al. 2007a). The wrist morphology would also be inconsistent with more advanced tool making and manipulative behaviors (Tocheri et al. 2007, 2008).

The Anatomically Based "New Species" Conclusion

Taken at face value, these morphologies suggest that *H. floresiensis* may have its closest affinity with a small-bodied hominin retaining aspects of anatomy that are primitive for the genus *Homo* (e.g., Morwood and Jungers 2009b). Cladistic analyses of 60 cranial, mandibular, and postcranial character states support a pre-*erectus* ancestor and result in two equally parsimonious cladograms (Argue et al. 2009). One places *H. floresiensis* between *H. rudolfensis* and the clade including *H. habilis* and all later hominins. The second places *H. floresiensis* between *H. habilis* and the clade including *H. georgicus* (Dmanisi) and all later hominins. If either variant is correct, it would suggest that *H. floresiensis* is most closely related to hominins that lived more than 1.5 Ma. It would also suggest that pre-*erectus* hominins were the first to leave Africa, and this would challenge the traditional "Out-of-Africa 1" model for the first colonization of Eurasia by early African *Homo erectus*. However, cladistics is only one analytical technique, and an increasing number of recent analyses support *Homo erectus* as the ancestor of *H. floresiensis* (e.g., Baab et al. 2013; Kubo et al. 2013) and insular dwarfism over ~1 Ma as the evolutionary process responsible for its unique mosaic morphology (see below).

Could *Homo floresiensis* Be a Pathological Modern Human?

The alternative major hypothesis that *H. floresiensis* is a pathological modern human suffering microcephaly and disordered growth appeared shortly after the introduction of the taxon in 2004. Henneberg and Thorne (2004) argued that such pathologies could not be rejected as an explanation, particularly in view of the fact that this explanation was more consistent with the age of the site and the associated artifacts, which are found elsewhere in Island Southeast Asia in association with modern humans (see also Brown and Morwood 2004). This work was followed by a more extensive analysis by Jacob et al. (2006), which has been largely discredited based on the extensive morphological analyses of *H. floresiensis* (e.g., thin-walled, "tublated bone" or weak muscles). Some features have also been shown to fall within the range of variation of normal humans or apes (e.g., asymmetry) (Baab and McNulty 2009; Larson et al. 2009; Kaifu et al. 2009). There is, however, a relatively large literature supporting a pathological interpretation for *H. floresiensis* (e.g., Weber et al. 2005; Martin et al. 2006a, b; Martin 2007; Richards 2006; Henneberg 2007; Hershkovitz et al. 2007, 2008; Tuttle and Mirsky 2007; Rauch et al. 2008; Obendorf et al. 2008; Oxnard et al. 2012).

The various syndromes that have been proposed to explain *H. floresiensis* include (1) a combination of growth hormone-insulin-like growth factor I axis modification and mutation of the MCPH (microcephalin) gene family (Richards 2006), (2) Laron syndrome (Hershkovitz et al. 2007, 2008), (3) microcephalic osteodysplastic primordial dwarfism type II (MOPD II) (Rauch et al. 2008), and (4) myxedematous endemic (ME) cretinism (Obendorf et al. 2008; Oxnard et al. 2012). All these can produce short stature and/or microcephaly, but the majority have been rejected on the basis that they do not account for the total morphological pattern observed in *H. floresiensis* (e.g., Falk et al. 2008, 2009a; Brown and Maeda 2009).

The most recent debate surrounds ME cretinism (Obendorf et al. 2008; Oxnard et al. 2012; Brown 2012). ME cretins are born without a functioning thyroid due to environmental factors including iodine deficiency, selenium deficiency, and raised serum thiocyanate (Oxnard et al. 2012). These authors argue that ME cretinism is known in Island Southeast Asia, on Bali, Java, Sumatra, and Borneo, and can be found in modern populations living as close as 18 km to the ocean and iodine-rich marine resources. They also note that this condition results in extreme dwarfism and a mosaic of skeletal features, particularly in younger individuals, that is "rather like" the mosaic found in *H. floresiensis*.

Proponents of this hypothesis, although vigorous in its support, have not had the opportunity to study the original *H. floresiensis* material, and equally vigorous critics argue that many of the features used in its support, such as a persisting bregmatic fontanel, a depressed nasal bridge, absence of a frontal sinus, and a bipartite trapezoid, do not hold up to scrutiny (Falk cited in Dalton 2008; Jungers et al. 2009a; Brown 2012). Brown (2012) notes that out of the large number of skeletal and dental traits associated with ME cretinism in the clinical literature, only very short stature and the degree of humeral torsion are shared with *H. floresiensis*, and a similar humerus torsion angle is also found in earlier members of the genus *Homo* (see also Larson, 2007). Brown (2012) emphasizes that there is no evidence in *H. floresiensis* of delayed linear growth and development characteristic of ME cretins and that the average brain size of cretins is within the normal human range.

As emphasized by Aiello (2010), the fact that existing hypotheses for pathological explanations for LB1 cannot explain the evidence does not falsify all potential hypotheses. Knowledge of the skeletal manifestations of the various syndromes resulting in dwarfism and microcephaly has increased in recent years, but without more conclusive comparative information, and wider access to the original *H. floresiensis* fossils, definitive DNA analyses, and/or additional discoveries, the weight of the current evidence continues to support the hypothesis that *H. floresiensis* is a surviving species of early *Homo*.

Questions Raised by the "New Species" Interpretation of *Homo floresiensis*

In many ways the "new species" interpretation of *H. floresiensis* is inconvenient. This is because it raises more questions about *H. floresiensis* and human evolution in Island Southeast Asia than it answers, some of which are summarized in Aiello (2010). It would be much easier to write off *H. floresiensis* as an interesting pathological modern human.

One major question is the relationship of *H. floresiensis* to other Asian hominins such as the Denisovans and modern humans. Genetic evidence suggests that the Denisovans were once a large, widespread population, and Stringer (2012) speculates that perplexing Asian hominins such as Maba, Xujiayao, Dali, and Jinniushan in China and Narmada in India may be Denisovans. These hominins are probably too recent in time to be ancestors of *H. floresiensis*, but the presence of Denisovan DNA in indigenous Australians, Papua New Guineans, and other Island Southeast Asian populations suggests that the Denisovan range extended across Wallace's Line (Reich et al. 2011; Pennisi 2013; Cooper and Stringer 2013). This also suggests that *H. floresiensis* could have been contemporaneous in this region at various times with both the Denisovans and modern humans (see O'Connor 2007, for modern human occupation in Island Southeast Asia). Their isolation on Flores may have been due to the strong currents between islands, and non-endemic faunal evidence suggests that modern humans were not moving freely among the islands until well into the Holocene (Van den Bergh et al. 2009).

This raises the issue of when and how *H. floresiensis* could have arrived on Flores. The archaeological evidence from Wolo Sege at 1.02 ± 0.02 Ma (Brumm et al. 2010) and Mata Menge at 800–880 ka (Morwood et al. 1998; Brumm et al. 2006; Moore and Brumm 2007) in the Soa Basin suggests that the island had been occupied for at least a million years. Archaeological continuity between these sites and Liang Bua also implies population continuity. However, the best evidence may come from the fauna (Van den Bergh et al. 2009; Meijer et al. 2010; Dennell et al. 2013). Throughout the majority of this period, the fauna is described as an impoverished endemic island fauna, lacking evidence of new colonizers. Van den Bergh et al. (2009) report a faunal turnover at approximately 900 ka, after which time the fauna remains endemic until ~17 ka and the volcanic event associated with the disappearance of *H. floresiensis* and the dwarfed *Stegodon* (*Stegodon florensis insularis*). The consensus is that the ancestor of *H. floresiensis* must have arrived on Flores via a sweepstakes event (such as a tsunami) and the prevailing currents suggest Sulawesi as a probable source (Van den Bergh et al. 2009; Meijer et al. 2010; Dennell et al. 2013). Dennell et al. (2013) also concludes on the basis of energetic modeling that a small-bodied, energetically efficient hominin could have survived on an island of the size of Flores throughout this period (see also Meijer et al. 2010).

But who was the ancestor of *H. floresiensis*? There is currently no clear evidence to indicate whether it was *Homo erectus* or an unknown pre-*erectus* hominin. Meijer et al. (2010) agree with the original interpretation (Brown et al. 2004) and argue that the only plausible ancestor would have been *Homo erectus*, who is the sole currently known hominin that was present in Island Southeast Asia prior to a million years ago. Meijer et al. (2010) explain the mosaic morphology of *H. floresiensis* as a consequence of insular evolution, and these authors suggest that it follows evolutionary pathways similar to those of other terrestrial vertebrates in island environments. They specifically invoke pedomorphosis to explain the presence of features in *H. floresiensis* that are primitive for *Homo erectus*. They also agree with Taylor and van Schaik (2007), Weston and Lister (2009), and Kubo et al. (2013) in arguing that the degree of brain size reduction in *H. floresiensis* would be possible, and might even be expected, under conditions of resource limitation in an island environment (see also Migliano et al. 2007; Bromham and Cardillo 2007 for body size reduction).

This is a parsimonious explanation, but at present, much needs to be taken on faith. It is unknown whether insular dwarfing of *Homo erectus* would result in the unique mosaic of features recognized in *H. floresiensis*. However, the alternative "new species" hypothesis involving a pre-*erectus*, smaller-brained antecedent has its own difficulties. It would be paradigm changing in postulating the existence of an unknown pre-*erectus* hominin in eastern Asia prior to one million years ago. However, the history of human evolutionary research has shown that anthropologists are naive to believe that all of the hominin species that have ever existed are known today (Aiello 2010). Based on the morphology of *H. floresiensis*, the alternative "new species" hypothesis that postulates an unknown pre-*erectus* ancestor must continue to be entertained as a plausible explanation for *H. floresiensis* evolution. As Dennell and Roebroeks (2005) suggest, it is possible that *H. floresiensis* will result in a major transformation in our understanding of the course of human evolution in Asia. A resolution to this issue awaits further research and discovery.

Conclusion

The controversies surrounding *Homo floresiensis* have focused attention on a variety of issues relevant to the interpretation of the fossil evidence for human evolution. Prime among these is the evidence necessary to separate normal from pathological morphology and conclusively decide whether particular fossil material merits recognition of a new species. This is particularly important in cases where the new species appears to be out of either time or place. The case of *Homo floresiensis* is particularly perplexing because the morphology suggests affinities with Pliocene or early Pleistocene hominins from Africa (e.g., *Au. afarensis*, *H. habilis*), but the species persists on Flores at a time that is contemporaneous with modern humans and long after other hominin species went extinct. This is not the first time in the history of human origins research that new discoveries have raised such questions. For example, the discovery of the Neanderthals, *Pithecanthropus*, and the Taung child (*Au. africanus*) raised similar debates in their day (Aiello 2010). In these cases, additional fossil material and analytical research ultimately settled the debate in favor of new species and radical changes in our understanding of the course of human evolution.

The question is whether the same will happen in the current case of *H. floresiensis*? There is only one cranium (LB1) giving evidence of the relatively small brain size and one skeleton (LB1) that is complete enough to determine body proportions and the other features making up the unique *H. floresiensis* mosaic of primitive and derived features. There is a second partial skeleton (LB6), including a mandible, which confirms that at least some of the morphology is found in more than one individual. The remaining *H. floresiensis* hypodigm is largely fragmentary, and although it does document some of the unique *H. floresiensis* features, it is largely ignored by recent proponents of the "pathological modern human" hypothesis. One reason for this may be that they have not had the opportunity to study the original fossil material.

At present, the various syndromes that have been evoked to explain *H. floresiensis* as a pathological modern human have not been able to account for its total morphological pattern. As a result, the "pathological modern human" hypothesis cannot be supported. The weight of the evidence currently supports the "new species" hypothesis, and of the alternative possible *H. floresiensis* ancestors, currently the most parsimonious is an early Asian *Homo erectus* that would have been present at the right time and place in Island Southeast Asia (Meijer et al. 2010). The major obstacle to the idea that *H. floresiensis* is a dwarfed descendant of *H. erectus* has been brain allometry, although based on recent research, this obstacle may be receding (Kubo et al. 2013). However, major questions still remain in relation to whether the total pattern of *H. floresiensis* morphology is consistent with this hypothesis and whether *H. floresiensis* could have survived on Flores for over 1 Ma. There are also concerns over its relationship to other contemporaneous hominins, including modern humans. We also know little about its physiology, life history, locomotion, and lifestyle, and there remain many questions about its cognitive capabilities in relation to the associated material culture (see Aiello 2010). Resolution to all of these questions will not happen until conclusive evidence appears in the form of additional fossil material, analytical advances, and ideally ancient DNA evidence. The *H. floresiensis* story does not yet have an ending.

Cross-References

- ▶ Defining the Genus *Homo*
- ▶ Hominoid Cranial Diversity and Adaptation
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ Later Middle Pleistocene *Homo*
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Modern Humans
- ▶ Postcranial and Locomotor Adaptations of Hominoids
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Paleodemography of Extinct Hominin Populations

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Origin of Modern Humans

Günter Bräuer

Contents

Abstract

In the early 1980s, a new period in the debate on modern human origins began, focusing on two alternatives: the Multiregional Evolution model and the Out-of-Africa hypothesis. Over the last few decades, new hominin discoveries, absolute dating, and other evidence have supported the latter view, which proposes a recent common origin of modern humans in Africa. The increasing evidence made the idea of long-term regional evolution up to modern humans in Europe and Asia, following the first expansion out of Africa at nearly 2 Ma, more and more unlikely. Only the African fossil record documents a continuous early modernization process. In contrast, the European evidence shows a replacement of the Neanderthals by modern humans. Also, the claimed evidence for regional continuity in China and Australasia has turned out to be unsubstantiated. Major questions in the current discussion of modern human origins refer to the fossil and molecular evidence for gene flow during the replacement period and to the number of species involved in Middle Pleistocene evolution.

G. Bräuer (✉)
Abteilung für Humanbiologie, Universität Hamburg, Hamburg, Germany
e-mail: guenter.braeuer@uni-hamburg.de

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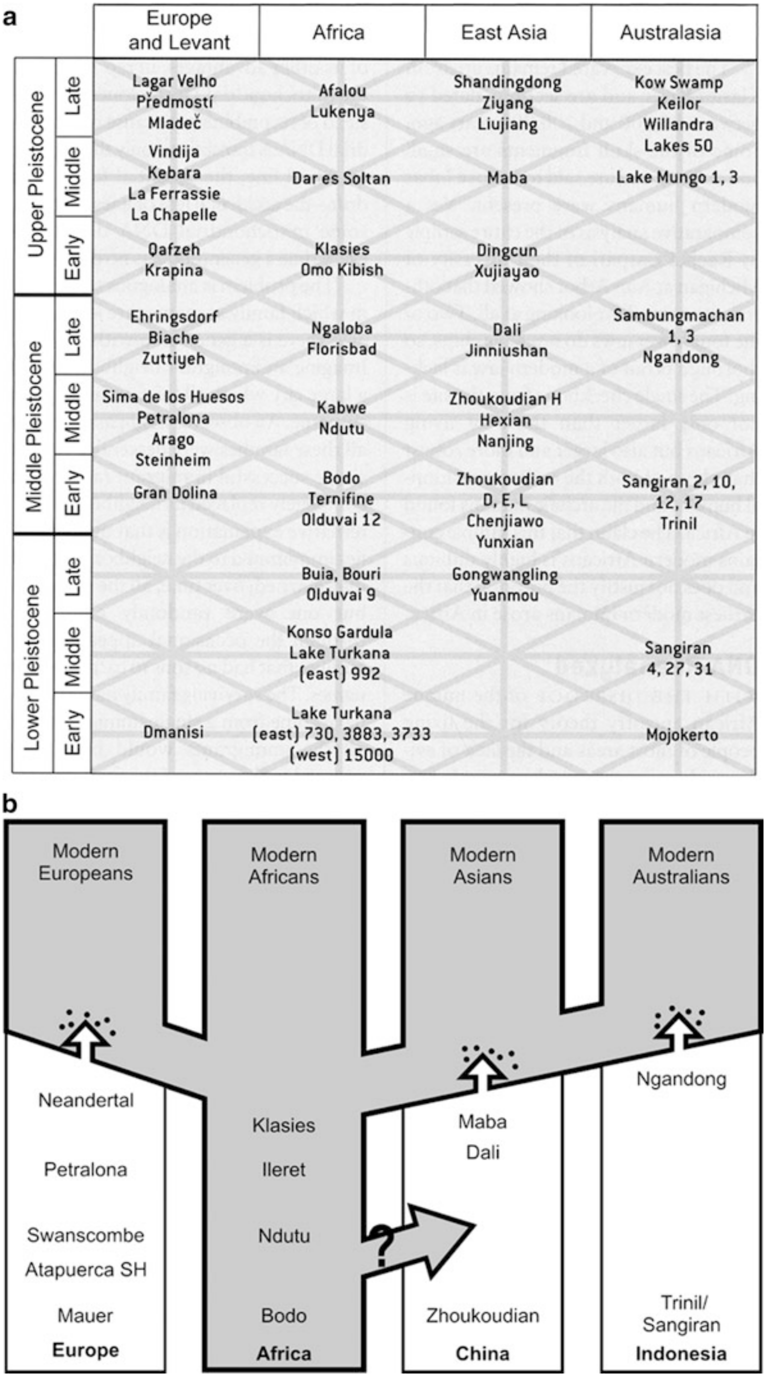
Early and Current Controversies

The origin of modern humans has always been a controversial topic in paleoanthropology. Already at the beginning of the twentieth century and based on a very sparse – mainly European – fossil record, alternative phylogenetic scenarios were suggested. Schwalbe (1906) proposed a unilinear concept in which Neanderthals were an intermediate form between Dubois' *Pithecanthropus* and modern humans. Boule (1913), on the other hand, saw the Neanderthals as an evolutionary cul-de-sac postulating a parallel "presapiens" lineage to modern humans. Although the Presapiens hypothesis became widely accepted in the subsequent decades, some researchers, especially Hrdlička (1927) and Weidenreich (1943), supported unilinear concepts. Weidenreich (1943), after examining the newly discovered Chinese and Javanese hominin fossils, proposed his Polycentric Evolution Theory, which suggested different evolutionary lines in North Asia, Southeast Asia/Australasia, Europe/Near East, and eastern/southern Africa. He regarded the regional sequences as an interconnected web evolving in a single common direction. Yet Weidenreich's (1947) explanation of orthogenesis as the driving factor of such a polycentric evolution was rejected by the new synthetic theory of evolution. In addition, Coon's (1962) later model of largely isolated parallel evolution in different parts of the world was eventually dismissed.

In the 1950s, new support emerged for the Presapiens hypothesis, in particular by the cranial remains from Fontéchevade in connection with the specimens from Swanscombe and Steinheim (Vallois 1954). However, later research on the critical presapiens specimens revealed their affinities to Neanderthals and Preneanderthals (Trinkaus 1981; Hublin 1982). In addition, new hominid discoveries, such as the partial crania from Arago and Biache St. Vaast, demonstrated that the idea of a separate lineage to modern humans in Europe was no longer tenable. It became clear that there was only one lineage in Europe leading to Neanderthals (Bräuer 1984a). During the 1950s, another model was proposed (Howell 1951) – the Preneanderthal hypothesis – which assumed that the lineages to Neanderthals and modern humans only split during the Eem Interglacial. Following this event, the southwest Asian "progressive" Preneanderthals evolved into modern humans, while the European Preneanderthals developed into the robust "classic" Neanderthals. However, this concept was also not supported by later research. No diachronic trends of reduction in size could be observed in the Near Eastern Neanderthals, and later dating revision revealed that early modern humans and Neanderthals were nearly contemporaneous in this region. Thus, by the late 1970s, the question of the origin of modern humans was again largely open. A few researchers such as Wolpoff (1980) continued to favor evolutionary continuity in Europe and elsewhere, whereas others like Howells (1976) assumed a recent common origin of modern humans.

In the early 1980s, a new period in the controversy on modern human origins began, mainly focusing on two alternatives: the Multiregional Evolution model and the Out-of-Africa hypothesis (Fig. 1). Wolpoff et al. (1984) proposed the Multiregional Evolution model, which was largely based on Weidenreich's theory



a

		Europe and Levant	Africa	East Asia	Australasia
Upper Pleistocene	Late	Lagar Velho Předmostí Mladeč	Afalou Lukenya	Shandingdong Ziyang Liujiang	Kow Swamp Keilor Willandra Lakes 50
	Middle	Vindija Kebara La Ferrassie La Chapelle	Dar es Soltan	Maba	Lake Mungo 1, 3
	Early	Qafzeh Krapina	Klasies Omo Kibish	Dingcun Xujiayao	
Middle Pleistocene	Late	Ehringsdorf Biache Zuttiyeh	Ngaloba Florisbad	Dali Jinniushan	Sambungmachan 1, 3 Ngandong
	Middle	Sima de los Huesos Petralona Arago Steinheim	Kabwe Ndutu	Zhoukoudian H Hexian Nanjing	
	Early	Gran Dolina	Bodo Ternifine Olduvai 12	Zhoukoudian D, E, L Chenjiawo Yunxian	Sangiran 2, 10, 12, 17 Trinil
Lower Pleistocene	Late		Buia, Bouri Olduvai 9	Gongwangling Yuanmou	
	Middle		Konso Gardula Lake Turkana (east) 992		Sangiran 4, 27, 31
	Early	Dmanisi	Lake Turkana (east) 730, 3883, 3733 (west) 15000		Mojokerto

Fig. 1 (**a**) Multiregional evolution (After Thorne and Wolpoff 2003, p. 52) and (**b**) Out-of-Africa models

of Polycentric Evolution. In contrast to Weidenreich's (1947) explanation of orthogenesis, the supporters of the new multiregional concept see a balance of evolutionary forces, such as gene flow, local selection, and drift, as explanations for the assumed long-term regional continuities (Wolpoff 1992). Yet they accepted and used most of Weidenreich's morphological observations for regional continuity that had been collected in the 1930s and 1940s (Wolpoff et al. 1984; Frayer et al. 1993). Although assuming interregional gene flow, multiregionalists have emphasized the regional pattern of evolution as stated, for example, by Frayer et al. (1993, p. 41): "Each geographic region we examined contains a wealth of information that shows the continuous evolution of *Homo* populations over time. We find neither specimens nor traits that could reflect an infusion of any African genes and their so-called more-modern morphology." Frayer (1992, p. 49) considered the "Neandertals as the probable ancestors of the people in the Upper Palaeolithic," and Thorne (1993, p. 173) is convinced that the "descendants of the Java and Peking people do not become extinct but give rise, without African influence, to the modern people of their region."

The roots of the alternative Out-of-Africa model can be traced back to the early 1970s. Although at that time practically all evidence from archaeology and paleoanthropology pointed to the presence of archaic hominins – the so-called "Rhodesioids" (named after the Kabwe cranium from Zambia) – in eastern and southern Africa from only 30 or 40 Ka (Clark 1970), new skeletal remains from Omo Kibish, Ethiopia, and new dates for the South African Border Cave specimens indicated the early presence of modern humans at about 100 Kyr bp, or even slightly earlier (Leakey et al. 1969; Protsch 1975). Yet it remained puzzling how such early moderns fit in with the much later presence of the archaic humans. Further research on the dating of the African Stone Age during the 1970s led to a drastic extension in time of the Middle and Later Stone Age and thus to older dates of the associated hominins (Clark 1979). It also turned out that the archaic "Rhodesioids" were considerably older than had been thought.

In the late 1970s, I started a new analysis of the Middle and Late Pleistocene hominin material from Africa. This research provided a new framework of *Homo sapiens* evolution, suggesting a mosaiclike, continuous anatomical process of modernization leading to an early emergence of modern humans. Based on this framework and a review of the fossil evidence from Europe and the Far East, I proposed an Out-of-Africa model initially dubbed the "Afro-European *sapiens*" hypothesis (Bräuer 1982) because the best evidence for replacement came from Europe. Yet the model was a global one, regarding replacement as the most likely process for the Far East as well (Bräuer 1984b). The Out-of-Africa model suggested an evolution to modern humans only in Africa and subsequent dispersals into Asia and Europe that replaced the resident archaic populations, including the Neanderthals. "Replacement" was assumed to also allow for interbreeding. In fact, a "Hybridization and Replacement model" was regarded to be in best agreement with the facts (Bräuer 1984b, p. 162). It could explain possible indications of regional archaic features among early modern humans, and it upheld the widely agreed upon view that the replaced archaic and the early modern humans belonged to the same species *H. sapiens*. A few years later, Cann et al. (1987) provided important support for a recent common origin of modern humans in Africa based on human mitochondrial DNA (mtDNA). Although no strongly divergent mtDNA lineages could be found among extant humans, Cann (1992, p. 71) did not assume reproductive isolation between the archaic and the dispersing modern populations, but rather concluded that we are about 30 Kyr too late to see the persistence of Neanderthal maternal lineages.

These and additional results from molecular biology and paleoanthropology during the 1980s supporting a Recent African Origin (RAO – a term also used for Out-of-Africa) did not lead to the dismissal of the alternative Multiregional Evolution model, but instead to a heated debate and an artificial polarization. The multiregionalists now claimed that the mtDNA results must be interpreted as excluding any gene flow and that this is an essential assumption of the Out-of-Africa model (Wolpoff and Thorne 1991). Although this view was rejected (Bräuer 1989, 1992; Stringer 1992), the multiregionalists focused on the criticism of the extreme "Eve Theory," assuming that by excluding gene flow, any possible indication of regional continuity outside Africa would be sufficient to disprove the Out-of-Africa model (Frayer et al. 1993). This argument, however, was misleading, as the "Eve" concept is based on a particular interpretation of the mtDNA data and cannot be equated with the Out-of-Africa model, which includes the evidence from fossils and nuclear DNA as well (Stringer and Bräuer 1994, p. 416). In fact, the Out-of-Africa replacement view allows for the possibility of gene flow between archaic and modern humans and is ready to accept any convincing evidence for it that might be found in the fossil record (Bräuer and Stringer 1997; Bräuer 2001a). Although subsequent research on the mtDNA did not provide any unequivocal evidence for interbreeding (Currat and Excoffier 2004), researchers like Serre and Pääbo *(*2006) were cautious and did not regard the extreme interpretation of complete replacement as proven. Only as recently as 2010 was the most relevant progress on the gene flow debate made. Sequencing of more than four billion nucleotides of the Neanderthal genome and comparisons to recent human genomes suggest that between 1 % and 4 % of the genomes of the people in Eurasia are derived from Neanderthals (Green et al. 2010, p. 721). Thus, not only fossil but also the molecular evidence supports such an "Out-of-Africa and hybridization" model (Stringer 2011), as was basically suggested about three decades ago (Bräuer 1984b, 2006; Stringer 2001a).

Another view on modern human origins is the so-called Assimilation model first proposed by Smith et al. (1989) that long held an intermediate position between the Out-of-Africa and Multiregional Evolution models by strongly emphasizing regional continuity in Central Europe and other peripheries (Aiello 1993; Frayer et al. 1993). More recently, this view has leaned toward the Out-of-Africa model but still assumes a more significant assimilation of the Neanderthals (Churchill and Smith 2000) than does the "Out-of-Africa and hybridization" model (Bräuer and Broeg 1998; Bräuer 2006). Most recently, the Assimilation model is said to even agree with a level of only 1–4 % of non-African contribution to extant Eurasians (Smith et al. 2012, p. 386). This would in fact mean that this latest perspective is now hardly distinguishable from the Out-of-Africa and hybridization model (Stringer 2011; Gibbons 2011). In the following paragraphs, the origin of modern humans in Africa and the controversy on the evolutionary pattern in the other parts of the Old World will be considered.

African Emergence of Modern Humans

Over the last few decades, the evolutionary framework of anatomical modernization and the early appearance of modern humans in Africa as basically suggested in the early 1980s (Bräuer 1984c) have gained increasing support (Klein 1999, 2009; Bräuer 2001b, 2012; Smith 2002; Stringer 2002a; Mbua and Bräuer 2012). Absolute dating evidence for several hominin specimens contributed to the current chronological framework of the process (Clark et al. 1994; Grün et al. 1996; Bräuer et al. 1997; McDougall et al. 2005; Brown et al. 2012). The evolutionary scheme presented here (Fig. 2) is based on quite a number of diagnostic as well as absolutely dated specimens that support a mosaiclike, continuously evolving lineage from archaic to modern humans. In spite of broad agreement on the African sequence (Klein 1999, 2009), there is some controversy on whether the different evolutionary groups or morphs should be distinguished on the species or, as suggested here, on the intraspecific level (Bräuer 2008).

The anatomical modernization process can be divided into three groups or grades of *H. sapiens*, each of which includes hominin specimens of a similar evolutionary level (Bräuer 1989, 2008, 2012). The specimens grouped within the early archaic *H. sapiens* category are derived relative to *H. erectus*, especially regarding their enlarged cranial capacity, more vertically oriented lateral walls, expanded frontal bone, less strongly angulated occipital bone, more vertically oriented upper scale of the occipital, higher temporal squama, and reduced development of the supraorbital and occipital tori. The late archaic *H. sapiens* is clearly more derived compared to the morphological pattern of the early archaics, especially evident in the large cranial capacity, the more reduced supraorbital torus, and the near-modern or modern face, including the canine fossa and inframalar incurvature. This grade of evolution is followed by anatomically modern *H. sapiens* with a fully modern morphology of vault and face. There is obvious continuity between the grades, which are best seen as a way of describing the levels of the modernization process. In this respect, the late archaics have also been designated as the transitional group (Smith 2002). This approach suggests neither anything about the underlying factors of anatomical modernization nor whether there are parts of the lineage that show more relevant changes toward the modern morphology than others. Thus, the identification of major structural elements in this process, such as neurocranial globularity and facial retraction (Lieberman et al. 2002), is relevant. Indeed, many of the features and aspects characterizing the grades are connected with such general changes (Mbua and Bräuer 2012).

A key specimen of early archaic *H. sapiens* is the Bodo hominin from Ethiopia, dated by Ar/Ar to ca. 600 Kyr bp (Clark et al. 1994). The large cranial capacity of

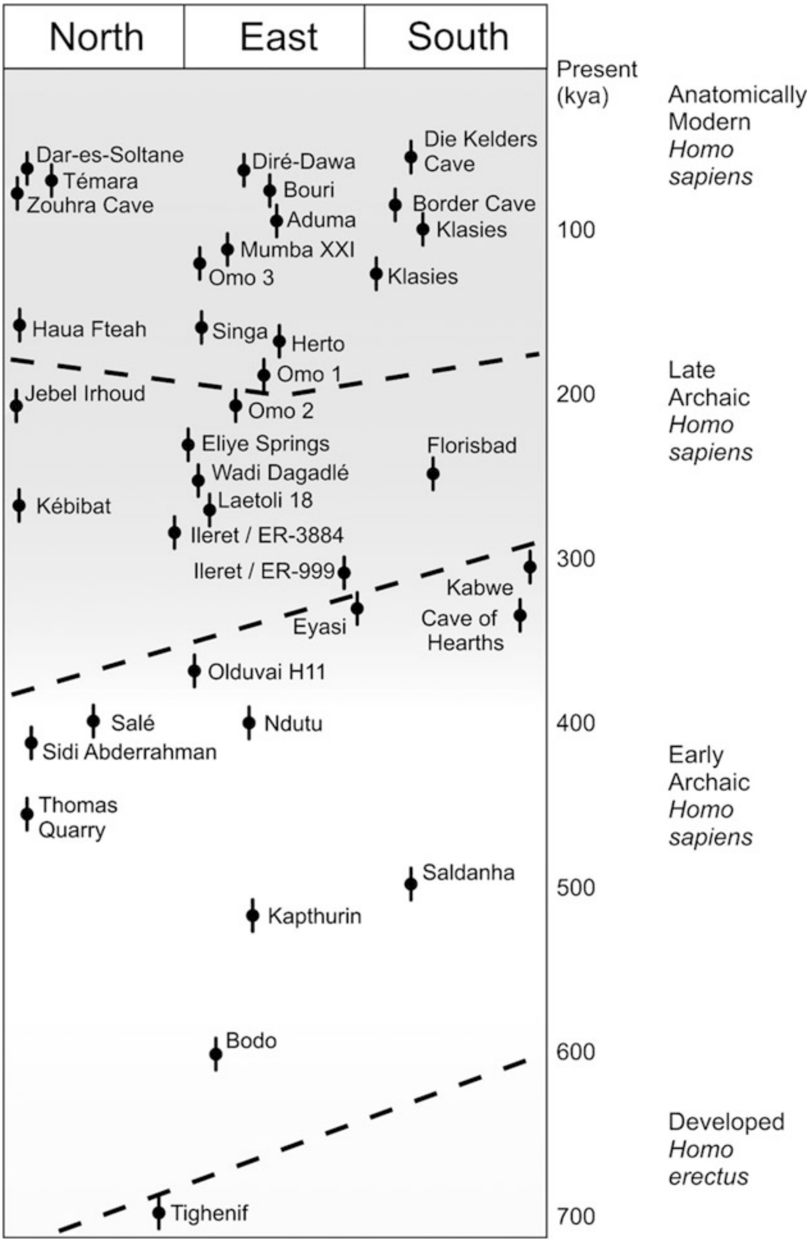


Fig. 2 Fossil record of *Homo sapiens* evolution in Africa

nearly 1,300 cm^3 is associated with some parietal bossing, a coronally expanded frontal, and derived features of the temporal. The supraorbital torus even shows some division into a medial and lateral portion. In the still massive face, there are several characteristics shared with modern humans (Rightmire 1996). Another specimen of similar or slightly younger age (Klein 2009) is the Saldanha (or Elandsfontein) cranium from South Africa. Having an estimated cranial capacity of around 1,225 cm^3, the parietals are well arched and show some bossing. Also, the frontal squama is coronally enlarged and the supraorbital torus attenuates laterally. The occipital is less angulated than generally seen in *H. erectus* and the transverse torus is reduced. The other well-preserved early archaic specimens, such as the crania from Kabwe, Zambia; Eyasi and Ndutu, Tanzania; and Salé, Morocco, date from the same time period between 600 and 300 Ka and exhibit similar derived *sapiens*-like conditions in spite of obvious individual variation (Bräuer 2008, 2012; Mbua and Bräuer 2012).

The late archaic transitional group also comprises specimens spreading from northern to southern Africa. A good example of these near-moderns is the cranium KNM-ER 3884 from Ileret, East Turkana (Fig. 3) directly dated by U/Th gamma-ray spectrometry to ca. 270 Kyr bp (Bräuer et al. 1997). A previous analysis showed that most of the cranial vault falls close to the range of Holocene Africans (Bräuer et al. 1992a). However, the cranium also exhibits a continuous but moderately developed supraorbital torus that deviates from the generally rather modern impression of the specimen (Bräuer 2001b; Schwartz and Tattersall 2003). Further support for such an early presence of near-modern late archaics came from absolute dates

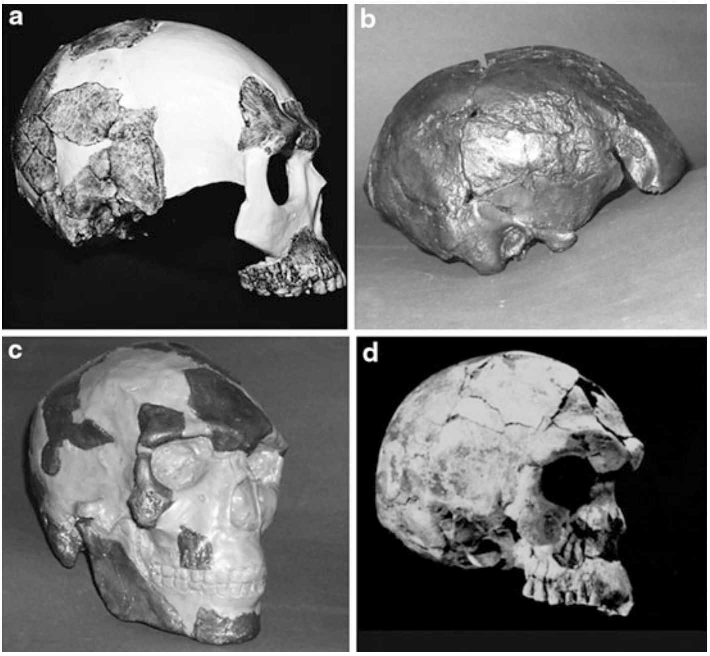


Fig. 3 Late archaic and early modern *Homo sapiens*: (**a**) KNM-ER 3884, Ileret; (**b**) Omo Kibish 2; (**c**) Omo Kibish 1; (**d**) BOU VP-16/1, Herto (After White et al. 2003, p. 734)

for the Florisbad hominid from South Africa and for the Laetoli Hominid 18 from the Ngaloba Beds in Northern Tanzania (Manega 1995; Grün et al. 1996). The Florisbad specimen directly dated by ESR to ca. 260 Kyr bp has a coronally greatly expanded frontal bone associated with a continuous but only slightly projecting supraorbital torus and a modern facial shape with a well-developed canine fossa. The LH 18 cranium, with an age of more than 200 up to 300 Kyr, exhibits a modern-looking face with a canine fossa and a near-modern braincase with a capacity of about 1,350 cm^3, a more or less rounded occipital bone, and well-developed parietal bossing. Archaic features mainly include the flat and narrow frontal squama and the supraorbital torus (Bräuer 1989). However, the relatively thick torus shows an incipient division in the midorbital region, which might be a tendency toward the fully modern pattern. Based on its combination of ancestral and derived conditions, the cranium from Eliye Springs, West Lake Turkana, might also belong to this grade (Bräuer and Leakey 1986; Bräuer et al. 2004a). Important late archaic crania also come from Jebel Irhoud, Morocco, dated to about 170 Kyr bp (Grün and Stringer 1991; Hublin 1992; Bräuer 2012).

The mosaic-like transition from late archaic to early anatomically modern *H. sapiens* is also obvious in the available specimens from Ethiopia such as the Omo Kibish remains (Fig. 3). Recent fieldwork at the sites and Ar/Ar dating has suggested that both the Omo 1 skeleton and the Omo 2 cranium date to 195 ± 5 Kyr bp (McDougall et al. 2005; Brown et al. 2012). Whereas the Omo 1 specimen is by most accounts fully anatomically modern and according to the new dating evidence the oldest known modern human, the Omo 2 cranium shows a mosaic of modern and archaic features. It exhibits a robust yet basically modern supraorbital morphology along with strong midsagittal keeling and an angulated occipital bone. Recently discovered cranial remains from Herto in the Middle Awash, Ethiopia, dated by Ar/Ar to ca. 154 – 160 Kyr bp, further illustrate this transitional process (White et al. 2003). The large robust Herto cranium BOU VP-16/1 (Fig. 3) apparently exhibits a modern supraorbital morphology and modern face combined with a rather angulated occipital bone similar to the condition seen in Omo 2. The variability of this occipital trait, however, is evident in the less angled condition of the more fragmentary adult specimen BOU VP-16/2 (White et al. 2003). With an age of around 150 Kyr bp, the Singa cranium from Sudan also belongs to this earliest modern human spectrum (Bräuer 2012).

More early moderns come from South Africa, especially from the Klasies River Mouth Caves. Here, the oldest human remains date to ca. 120 Kyr bp. These maxillary fragments fall within the range of variation of Holocene Africans (Bräuer et al. 1992b). A nearly complete mandible with an age of about 100 Kyr is anatomically modern, as are the other slightly more recent cranial fragments from the site (Bräuer 2001b, 2008). Regarding the postcranial specimens, the conditions seen in the Klasies remains can be matched with recent population samples from southern Africa (Rightmire and Deacon 1991; Churchill et al. 1996). Some features, such as the relatively low coronoid height of the ulna, could be retained archaic features reflecting the mosaic pattern of evolution in the postcranial skeleton (Churchill et al. 1996). But it is also possible that such postcranial conditions simply belong to the range of variation of these early modern humans (Pearson 2000). Another early modern specimen from South Africa is the Border Cave 1 partial cranium, which is about 90 Kyr old or perhaps somewhat older (Grün and Beaumont 2001).

Considering the complete evidence from the fossil record, of which I can discuss only a few specimens here in some detail, it is obvious that there is good documentation of the modernization process in Africa. This process recently gained further support from a new analysis of the Middle Pleistocene hominins showing clear trends from early archaic up to modern *H. sapiens* in many metrical and nonmetrical cranial features (Mbua and Bräuer 2012). The current fossil record of the African Middle Pleistocene allows subdivision into the three suggested groups, regardless of whether they are termed "grades" of an evolving species *H. sapiens* or different "morphs." Foley (2001), however, distinguishes these groups on the species level, as *H. heidelbergensis*, *H. helmei*, and *H. sapiens*. Yet he concedes that the derived descendant taxa of *H. heidelbergensis* are problematic because of the continuity that can be found between them and their presumed ancestor:

> These seem to be species in the sense that Simpson meant – lineages with independent trajectories – but both the details of the fossil record and the scale of the process seem to rule out any punctuated events. Indeed, continuity between them, rather than discontinuity, is the reason for the persistent problem of delimiting the taxonomic units in the later stages of human evolution and gives rise to the question of whether the species concept, which lies at the heart of macroevolutionary theory, is sufficiently fine-tuned to cope with evolution at this scale. (Foley 2001, pp. 9–10)

However, problems already exist with regard to *H. heidelbergensis*. Shortly after Adefris (1992) classified the Bodo cranium as "archaic *Homo sapiens*" based on a detailed study, Rightmire (1996) considered it more reasonable to refer to Bodo as a *H. heidelbergensis*. Rightmire (1998) suggested speciation between *H. erectus* and *H. heidelbergensis* in Africa at around 800 – 700 Ka, instead of a speciation between *H. erectus* and (archaic) *H. sapiens* (Bräuer 2001b). While this difference appears to mainly involve names, especially since Rightmire also favors a single polytypic species *H. erectus* in Asia and Africa, his scheme also suggests two further speciations: one in Europe from *H. heidelbergensis* to *H. neanderthalensis* at ca. 300 Ka and another in Africa from *H. heidelbergensis* to *H. sapiens* at ca. 150 Ka. However, due to the mosaic nature of the accretion process in Europe, it is hardly possible to define any clear divisions along the Preneanderthal/Neanderthal lineage (Hublin 1998, p. 302; Klein 2009). Thus, there appears to be little convincing evidence for such a speciation within the European record. In Africa, there is a similar process with regard to the mosaiclike modernization, which also does not justify any subdivisions at the species level (Smith 2002; Turbón 2006; Bräuer 2008). I think it is more likely that we are dealing with one evolving biological species and several subspecies (Jolly 2003). Further splitting of the African sequence as suggested by Foley and Lahr (1997) into three species (*H. heidelbergensis*, *H. helmei*, and *H. sapiens*), which largely include the same African specimens as the three proposed grades, can only mean that these are artificially defined morphs or paleospecies. Yet it is problematic that Foley and

Lahr (1997) also included European fossils in *H. helmei*, as outlined by Stringer (2002a, p. 567).

First, Neanderthal characteristics were already evolving in Europe prior to the hypothesized appearance of "*H. helmei*," e.g., in the Swanscombe specimen, dated to ca. 400 Kyr bp. Second, African specimens such as Florisbad and Jebel Irhoud make unparsimonious ancestors for the Neanderthals, since not only do they post-date the appearance of Neanderthal clade characters in Europe, but they appear to lack Neanderthal morphological characteristics that might be expected in a common ancestor.

Recently, Weaver (2012) demonstrated that models based on theory of population and quantitative genetics are well in agreement with a lengthy process of modern human origins that lasted from the divergence of the modern human and Neanderthal evolutionary lineages more than 400 Ka to the expansion of modern humans out of Africa, without speciation events. In spite of the current discussion on the number of taxa involved (Bräuer 2008, 2012), there is nearly general agreement on a post-*erectus* evolutionary process in Africa leading to an early origin of modern humans during the late Middle Pleistocene. This is in agreement with the fact that in the Near East, anatomically modern humans appeared as early as about 100–130 Ka. These early moderns from Skhūl and Qafzeh might not only have an African origin but may also represent the oldest, well-documented evidence of modern humans outside of Africa. Interestingly, and not yet fully understood, these moderns might have coexisted in the Near East with Neanderthals for some tens of thousands of years until the latter disappeared at around 45 Ka. According to both morphological and the recent molecular evidence, gene flow occurred during this period of coexistence (Bräuer and Rimbach 1990; Green et al. 2010).

Replacement of European Neanderthals

Largely parallel to the anatomical modernization process in Africa, the evolution of the Neanderthals took place in Europe. It is widely agreed that the development of the Neanderthal morphology mainly resulted from an accretion process, which began about 400–530 Ka (Hublin 1998; Bischoff et al. 2003; Stringer 2012). Studies on whole Neanderthal mtDNA genomes support such a long, separate evolution in Africa and Europe (Briggs et al. 2009; Endicott et al. 2010). Recent estimations of the human-chimpanzee split using generation times in great apes could also point to a somewhat earlier population split between Neanderthals and modern humans (Langergraber et al. 2012). This does not necessarily indicate that two different biological species originated since the taxonomic significance of the genetic differences is ambiguous (Hublin 1998; Jolly 2003), and as Hofreiter (2011, p. 7) put it: ". . ., given that humans and Neanderthals are large-bodied mammals with long generation times, the recent divergence time of humans and Neanderthals argues against species-level distinction." In view of the increasing evidence for widespread interbreeding between modern and different archaic humans (see below), Stringer (2011, p. 261, 2012) also pointed to the possibility of abandoning the different species names and lumping all these post-*erectus* fossils together as *H. sapiens*. So, whether one prefers to regard the Neanderthals as a subspecies of *H. sapiens* (Turbón 2006; Bräuer 2008) or as a different species or paleospecies (Tattersall and Schwartz 2000; Harvati 2003), the Neanderthals were clearly very closely related to us (Stringer 2001b). Of special relevance in this respect is also the research on possible Neanderthal-modern differences in life history. Current evidence, however, points to great overlap between dental development in Neanderthals and modern populations from different regions of the world and to great difficulties in gauging Neanderthal life histories from dental growth (Guatelli-Steinberg 2009). Nevertheless, the long, separate evolution of the Neanderthals led to an accumulation of a large number of derived features in the skull and postcranial skeleton that are either unique or most frequent in this group (Trinkaus 1988; Hublin 1998).

In spite of the numerous differences between the Neanderthal morphology and that of early modern Europeans, multiregionalists have long regarded Central Europe as a possible region of evolutionary change from Neanderthals to modern humans (Smith 1982; Frayer et al. 1993). In particular, the Neanderthal remains from Vindija, Croatia, were considered to demonstrate evolutionary continuity to early modern humans of the region, as, e.g., from Velika Pećina. However, direct AMS radiocarbon dating has shown that the frontal fragment from Velika Pećina once regarded to be ca. 34 Kyr old is only 5 Kyr old (Smith et al. 1999) and the most recent Vindija Neanderthal sample (G1) has an age of ca. 32 Kyr bp, based on a new ultrafiltration technique for bone radiocarbon samples (Higham et al. 2006). AMS dating has led to further drastic revisions regarding some presumably early modern Europeans. The frontal bone from Hahnöfersand near Hamburg, which was dated to ca. 36 Kyr bp (Berger and Protsch 1989, p. 64), has been redated to only 7,500 years bp (Terberger et al. 2001). For the fragmentary crania from Zlatý Kůn and Svitávka, Czech Republic, for which ages of at least 30 Kyr were suggested, new dates of 12,870 and 1,180 years bp, respectively, were obtained (Svoboda et al. 2002). Also, the human remains from the Vogelherd Cave in southwestern Germany, which have long been thought to derive from Aurignacian deposits, turned out to be only 5 Kyr old (Conard et al. 2004).

In spite of the exclusion of several presumably early modern Europeans, there are still a number of specimens that date to more than 30,000 and even somewhat more than 40,000 radiocarbon years bp (Mellars 2011). Among these are the remains from Mladeč, Czech Republic, for which direct AMS dating on several specimens provided ages of about 31 Kyr bp, i.e., 36 Kyr bp based on new calibration curves, which are in agreement with the Aurignacian artifacts as well as previous AMS dates for associated calcite deposits (Svoboda et al. 2002; Wild et al. 2005; Higham et al. 2011). Further early modern cranial and mandibular remains have recently been discovered in the Peștera cu Oase, Romania, for which direct AMS dating of a mandible yielded ages of 34–36 Kyr bp (Trinkaus et al. 2003) and recent redating using the ultrafiltration technique resulted in a calibrated date of ca. 40 Kyr bp (Higham et al. 2011). Ultrafiltrated collagen radiocarbon dating on animal bones associated with the presumably modern maxillary fragment Kent's Cavern 4 from England has even suggested calibrated dates between 42 and 44 Kyr bp (Higham et al. 2011; Stringer 1990). In spite of the recent use of the improved cleaning techniques of bone collagen to reduce contaminations, there is still good evidence for several thousand years of Neanderthal-modern coexistence. The question of a Neanderthal contribution to the early modern European gene pool has been strongly debated between supporters of the Multiregional Evolution, Assimilation, and Out-of-Africa models for many years.

Based on the current dates, the Mladeč remains represent the best preserved early modern material from the time at which Neanderthals were still around in Central Europe (Teschler-Nicola 2006). Thus, it is key material for examining the question of Neanderthal-modern gene flow. Multiregionalists have long used the Mladeč material to demonstrate regional evolution. Frayer (1986, p. 254) saw here "good evidence in support of a gradualist model," and Wolpoff (1999, pp. 762–763) described the Mladeč specimens 4, 5, and 6 as Neanderthal-like. In testing the similarities of Mladeč 5 and 6 to their potential ancestors – European Neanderthals and early moderns from Skhūl/Qafzeh – Wolpoff et al. (2001, p. 293; Wolpoff 2009) even found a predominance of Neanderthal resemblances for several sets of variables, which are said to separate the Neanderthal and Skhūl/Qafzeh samples.

In order to determine the hard evidence for the Neanderthal contribution to these early moderns, analyses of the Mladeč material were carried out (Bräuer and Broeg 1998; Bräuer 2006; Bräuer et al. 2006). These studies included the most relevant and well-preserved crania, the females Mladeč 1 and 2 and the males Mladeč 5 and 6 (Fig. 4) as well as the maxilla fragment, Mladeč 8. A set of nonmetrical Neanderthal

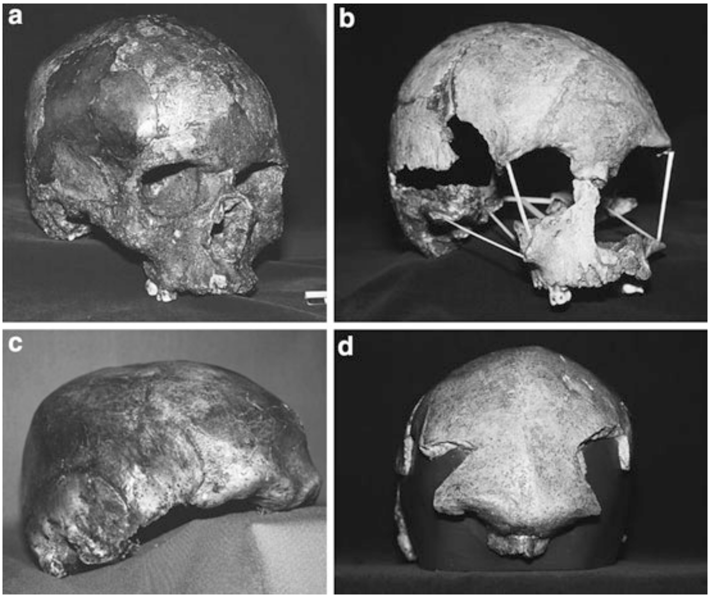


Fig. 4 Early modern crania from Czech Republic: (**a**) Mladeč 1; (**b**) Mladeč 2; (**c**) Mladeč 5; (**d**) Mladeč 6 (Photos **c**, **d**: H. Broeg)

features was used as well as measurements of the frontal shape and facial morphology and projection. The results were rather unexpected. Regarding the common nonmetrical Neanderthal features studied, not a single condition could be found in the Mladeč specimens that can be said to have been unequivocally derived from Neanderthals. On the contrary, the respective regions, such as the supraorbitals, the shape of the vault, the face, the occipital, and mastoid regions, are all anatomically modern and do not exhibit any derived Neanderthal morphology. Also, the metrical analysis revealed great deviations in the frontal curvature of the Mladeč specimens from both European and Near Eastern Neanderthals. Among the Upper Paleolithic sample ($n = 18$), Mladeč 1 and 5 show the greatest divergence from Neanderthals ($n = 10$). No indication of a midfacial projection could be found in these early Czech specimens. Mladeč 1, 2, and 5 diverge strongly from Neanderthals with regard to their Nasofrontal Angle (NFA), and Mladeč 1, the only specimen for which the Zygomaxillary Angle (SSA) could be determined, shows a large disparity when compared to the Neanderthal range of variation.

Major reasons for these contradictory results lie in the assessment as well as the selection of the features. For example, one of the commonly used features is the "occipital bun" (chignon), which exhibits a derived morphology in Neanderthals. In early modern Europeans, the occipital projections are not only placed "in the context of a rather different cranial shape" compared to that of Neanderthals (Churchill and Smith 2000, p. 97), but they also differ in a number of special details such as the extent of lambdoidal flattening, the angulation between the nuchal and occipital planes, and the height of the vertical face of the posterior occiput (Caspari 1991). These differences led Smith (1982) to suggest the term "hemibun" for the occipital projections in Upper Paleolithic specimens. Lieberman et al. (2000, p. 291) even raised the possibility that the specialized Neanderthal bun and the projections in early modern Europeans may not be homologous. In addition, these more moderate projections are rather variable and occur practically all over the world as, e.g., in Africa or East Asia (Bräuer and Broeg 1998; Wu 1998, p. 282). Thus, to label as an "occipital bun" anything different from the derived and well-defined Neanderthal bun leads to confusion, as can be well demonstrated in the case of the Mladeč specimens.

Wolpoff (1999, p. 762) classifies the occipital projections in Mladeč 5 and 6 as a "Neanderthal-like occipital bun," a view shared by Frayer (1992, p. 21). However, the midsagittal curvatures of Mladeč 5 and La Chapelle-aux-Saints are in fact more different than those of, e.g., Mladeč 5 and late Middle Pleistocene archaic *H. sapiens* specimens like Jebel Irhoud 1 or Laetoli H18 (Bräuer and Broeg 1998; Bräuer 2006). Smith et al. (1995, p. 201) had also emphasized that "the occipital buns in Jebel Irhoud are more similar to those in early modern Europeans (like Mladeč, Zlatý Kůn, or Predmosti) than to Neanderthals because of the greater similarity in posterior cranial vault morphology between them." Thus, there should be little reason to suggest that the more African-like hemibuns in Mladeč were derived from European Neanderthals. However, Frayer (1992, p. 21) argued that the morphology in the early modern Europeans must have derived from Neanderthals because occipital buns are not present in the Near Eastern early moderns. Yet, in regard to the bunning in Jebel Irhoud and other circum-Mediterranean specimens, Wolpoff (1999, p. 613) considers the bunning similar to Skhūl/Qafzeh. And indeed, comparisons of the midsagittal curvatures demonstrate close similarities between the occipital profiles of Qafzeh 6 and those of all three Mladeč crania in which the occipital is preserved (Bräuer 2006). Thus, the predominant multiregionalist assessment of the bun morphology in Neanderthals and Mladeč as present and in Skhūl/Qafzeh as absent is inaccurate.

Another example of problematic assessment concerns the "suprainiac fossa," which also has a clearly defined morphology in Neanderthals. It is a generally large, wide resorptive depression which is either rectangular or triangular in shape with a horizontal base formed by the transverse occipital torus (Nara 1994; Hublin 1998). Yet, as Caspari (1991, p. 184) pointed out, "it is unclear if all resorptive pitting in this area that could be referred to as fossae (or incipient fossae) can be validly compared with the Neandertal condition. Perhaps only the Neandertal pattern should be considered true suprainiac fossae, or alternatively some intermediate forms might also be considered suprainiac fossae." Quite obviously, not all pitting in this region can be regarded as a Neanderthal suprainiac fossa. Smaller or larger resorptive depressions that do not match the Neanderthal condition can be found in modern humans nearly everywhere in the world. They are frequently present, e.g., in terminal Pleistocene material from North Africa and occur in recent crania from New Guinea (Bräuer and Broeg 1998). These depressions normally have an inverted triangular shape with the apex pointing to the nuchal plane. Mladeč 5 shows such a small pitting, which can hardly be regarded as Neanderthal suprainiac fossa, and also Mladeč 6 exhibits a tiny non-Neanderthal-like depression. This had also been contended by Frayer (1986, p. 251), when he concluded that "neither Mladeč 6 nor 5 have a distinct suprainiac fossa." However, later Caspari (1991) felt that there was a suprainiac fossa in Mladeč 6, and Frayer (1992, p. 22), although emphasizing the differences between the Neanderthal and Upper Paleolithic conditions, recognized the structure in Mladeč 6 as a possible exception. This example also highlights the problematic use of character states in order to support the idea of continuity.

Wolpoff et al.'s (2001) finding of a great number of Neanderthal resemblances in two of the Mladeč specimens – which he recently repeated in more detail (Wolpoff 2009) – is largely based on features which are problematic with regard to both their assessment and phylogenetic relevance. Many of the nonmetrical features used are, in fact, metrical traits that were arbitrarily divided into two alternative conditions without any recognizable justification such as thick parietal at asterion (>9 mm), broad frontal (>125 mm), long frontal (glabella-bregma length >113 mm), or long occipital plane (>60 mm). With regard to other features used, it is unclear how they can be properly scored as present or absent without a clear scoring system. Among these are as follows: mastoid-supramastoid crests well separated, frontonasal suture arched, glabellar depression, glenoid articular surface flattened, and paramastoid crest prominent. In addition, many of the features used can hardly be regarded as distinguishing between Neanderthals and modern humans. Thus, it is not surprising that Wolpoff et al. (2001) found the most divergent numbers of differences between

Mladeč 5 and two closely related early modern specimens from Skhūl, i.e., only 8 differences to Skhūl 4, but 23 to Skhūl 5. Yet there are further problems with this study, such as the morphological representativeness of using only the male specimens, the lack of relevant features, and the inappropriate method of pairwise difference analysis (Collard and Franchino 2002; Bräuer et al. 2004b). Thus, critical reexamination of the claimed evidence for a considerable Neanderthal contribution in the Mladeč material cannot be supported.

Another early modern specimen claimed to show evidence for gene flow from Neanderthals is the mandible from Peştera cu Oase. However, according to Trinkaus et al. (2003, p. 11235), "the only feature that suggests Neandertal affinities is the lingual bridging of the mandibular foramen, a feature that is currently unknown among humans preceding Oase 1 other than the late Middle and Late Pleistocene members of the Neandertal lineage." Yet how reliable is this so-called H-O foramen for demonstrating Neanderthal-modern gene flow? As Smith (1978, p. 327) found, there are neither individuals under 18 years of age from any modern sample examined nor any juvenile Neanderthal exhibiting the H-O type. This makes it likely that, as Smith (1978) mentioned, factors developing during the individual's lifetime could also be responsible for the occurrence of the trait. Since the morphology at the mandibular foramen can change during a lifetime, the feature cannot be regarded as a good genetic trait (Lieberman 1995, p. 175). Moreover, its occurrence does not clearly signal continuity. According to Frayer (1992, p. 31), the H-O type appears in 10 out of 19 Neanderthals (52.6 %), in 4 out of 22 early Upper Paleolithic specimens (18.2 %), and in 2 out of 30 late Upper Paleolithic specimens (6.7 %). The four early Upper Paleolithic specimens, however, include the Neanderthal Vindija 207 and Stetten (Vogelherd) 1, which no longer belong to this group. Thus, there is no relevant occurrence of this feature in the early Upper Paleolithic. Moreover, most important in this respect is a study of terminal Pleistocene North African samples. Groves and Thorne (1999, p. 253) found the bilateral H-O foramen in 22.2 % of the Nubian material from Tushka and Jebel Sahaba, further showing that this trait is not necessarily derived from Neanderthals. Finally, the H-O foramen already occurred outside of Europe in *H. erectus* such as in OH 22 and Zhoukoudian H1. Thus, though it cannot be excluded, it is far from clear that this single possible Neanderthal trait present on one ramus of the Oase mandible really indicates gene flow from Neanderthals. There is also no unequivocal evidence for a Neanderthal contribution in the adolescent cranium Oase 2 that might be contemporaneous with the mandible. This specimen exhibits a whole set of derived modern features in the vault and face, combined with M3s that are unusually large and have a complex cusp pattern (Rougier et al. 2007). Specimens from two further Romanian sites have also been regarded as relevant to the gene flow debate. The mandible from the Peştera Muierii with an ultrafiltrated and calibrated AMS date of 34 Kyr bp (Higham et al. 2011) exhibits an asymmetrical mandibular notch which occurs most frequently in Neanderthals (Rak 1998; Soficaru et al. 2006). Yet it is also found in modern and recent humans as, e.g., in the Holocene Vogelherd mandible and shows great individual variability. Nevertheless, a possible indication to Neanderthal gene flow cannot be excluded here. This, however, appears less likely, regarding the nuchal morphology of the slightly younger calvaria from Cioclovina. Rather, this specimen shows a robust modern morphology and no typical Neanderthal suprainiac fossa (Bräuer 2010).

Finally, the juvenile Gravettian skeleton from Lagar Velho, Portugal, has been suggested to exhibit aspects indicating Neanderthal ancestry (Zilhão and Trinkaus 2002). Yet the major feature that has been suggested to show a Neanderthal-like condition – the relatively short lower legs – is not unequivocal. It cannot be excluded that the condition also reflects some adaptation among these early modern populations to cold conditions before the Last Glacial Maximum (Stringer 2002b) or individual variation within this modern population (Tattersall and Schwartz 1999). In addition, the occurrence of Harris lines points to periods of disease or malnutrition. Moreover, if one takes the estimated adult crural index for Lagar Velho of 80.7 % and the 95 % confidence intervals (77.5–83.9) as provided by Ruff et al. (2002, p. 380), there appears to be considerable overlap with early Upper Paleolithic Europeans as well. No matter whether some Neanderthal genes were involved in the specimens discussed here or not, it is difficult to escape the conclusion that the hard evidence points to only small traces of interbreeding between Neanderthals and modern humans. A Neanderthal contribution to early modern Europeans of up to 50 % as assumed by Wolpoff et al. (2004) has no support. Thus, a replacement process accompanied by a small amount of gene flow as suggested by the Out-of-Africa and hybridization model appears to be in good agreement with the current evidence from Europe (Bräuer 2010; Stringer 2011).

Continuity or Discontinuity in the Far East

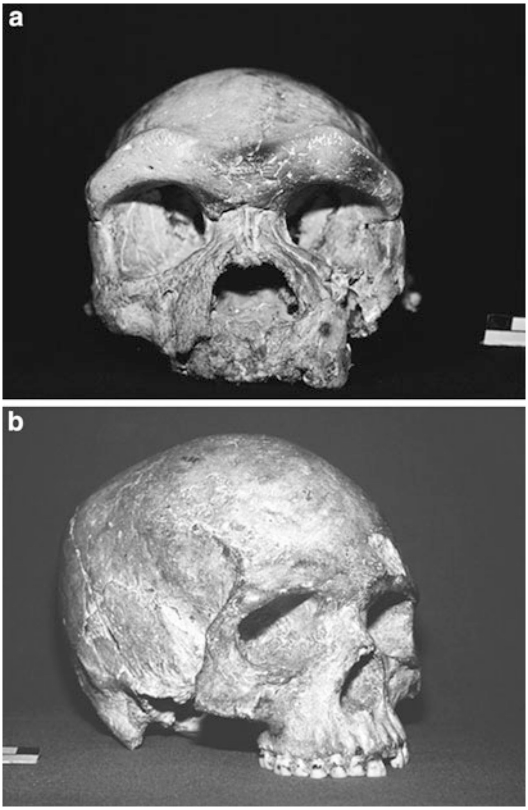
The assumption of regional evolution in China and Australasia is mainly based on morphological features or sets of features. Weidenreich (1943) published a list of 12 so-called Mongolian traits that he regarded as clear evidence for a close relationship between Chinese *H. erectus* and living north Chinese. Among these are midsagittal crest and parasagittal depression, metopic suture, Inca bone, certain "Mongolian" features of the nasal bridge and cheek region of the maxilla and zygomatic bone, shovel-shaped upper lateral incisors, and horizontal course of the nasofrontal and frontomaxillary sutures. Coon (1962, p. 458) was also convinced that many common features existed between Peking Man and living northeast Asians. Finally, the multiregionalists, as well, see strong support for their model in North Asia. Accepting most of the features suggested by Weidenreich and some other authors, multiregionalists presented a rather long list of assumed regional Chinese traits (Wolpoff et al. 1984; Pope 1992; Wu 1992). Although some features are said to have changed over time, Wolpoff et al. (1984, p. 435) were convinced that "all of these characteristics have much lower frequencies and are distributed discontinuously in regions other than China."

Weidenreich (1943) also saw an evolutionary line leading from *Pithecanthropus* via *H. soloensis* to the Australian aborigines of today. Some years before, Keith (1936) had already regarded the recently discovered Solo hominins as representing the evolutionary stage linking *Pithecanthropus* to the Australian aborigine. Wolpoff et al. (1984, pp. 443–444) mentioned about 20 continuity features of the cranium, including flatness of the frontal in sagittal plane, distinct prebregmatic eminence, marked prognathism, persistence of the zygomaxillary ridge, eversion of the lower border of the malar, rounding of the inferolateral border of the orbit, prelambdoidal depressions, and lambdoidal protuberance. Most of the features are from Weidenreich (1943), Larnach and Macintosh (1974), and Thorne and Wolpoff (1981). Based on these assumed regional features, multiregionalists are convinced that Australasia shows a clear anatomical sequence between the earliest Indonesian *H. erectus* and the recent and living Australians uninterrupted by African migrants at any time (Frayer et al. 1993, p. 21).

Since many of the regional features for the Far East were suggested in the first half of the twentieth century, reexaminations have been carried out by several authors over the last two decades. With regard to the suggested East Asian traits, Groves (1989, p. 279) arrived at the conclusion that there is "little evidence for special likeness of modern 'Mongoloids' to *Homo erectus pekinensis*" and identified many of the features as primitive retentions also found outside the region. According to Habgood (1992, p. 280) "none of the proposed 'regional features' can be said to be documenting 'regional continuity' in east Asia as they are commonly found on modern crania from outside of this region . . ., and are consistently found on archaic *Homo sapiens* and/or *Homo erectus* crania throughout the Old World." In her analysis of 11 proposed East Asian continuity features, Lahr (1994) found that almost all of them occurred *more frequently* in recent samples from other parts of the world. Facial flatness was found to be most pronounced in final Pleistocene populations from Northern Africa. A later detailed study by Koesbardiati (2000) focused on the middle and upper facial regions especially regarded as showing a great number of East Asian continuity features (Pope 1992; Frayer et al. 1993). The results, however, revealed that no variable showed a distribution as would be predicted by the Multiregional Evolution model. Instead, most of the features occur more frequently or are more pronounced among population samples from Africa, Europe, and Australia than in the Chinese sample. Some of the features show the highest frequencies among the Inuit of Greenland who, however, represent a relatively young population showing adaptations to extreme conditions (Howells 1993; Lahr 1995).

Also, the fossil record from China hardly supports regional continuity from *H. erectus* to modern people of the area. Even the problematic continuity features are lacking in archaic *H. sapiens* specimens. For example, the 200 Kyr old cranium from Jinniushan does not exhibit any of the following: midfacial flatness, a marked angulation of the maxilla and zygomatic bones when viewed from beneath, a flattened nasal saddle, a nondepressed nasal root, or lack of wisdom teeth. Based on further features, even Pope (1992) has raised doubts whether this hominin along with the Maba specimen fits into the picture of regional evolution in China and suggested strong genetic influence from the West into China in the terminal Middle or Late Pleistocene. Moreover, the 150–200 Kyr old cranium from Dali (Fig. 5) with its heavy supraorbital torus and other archaic features hardly reveals clear

Fig. 5 Archaic and early modern crania from China: (**a**) Dali; (**b**) Liujiang



similarities to modern Chinese. Because of the discontinuity between Chinese *H. erectus* and this East Asian archaic *H. sapiens* group and the similarities of the latter to archaic *H. sapiens* from Europe, it has been suggested that the Dali-Maba-Jinniushan morph has its roots in the archaic *sapiens* of the western part of the Old World. Recent sequencing of the genome of a 40 Kyr old finger bone from the Denisova Cave in the Altai Mountains, southern Siberia, identified a new archaic hominin group that shared some of its history with Neanderthals and might have split from the common Preneanderthal lineage some 200–300 Ka (Reich et al. 2010). Moreover, it has been shown that these so-called Denisovans interbred with the modern ancestors of present-day Melanesians and Australians, most likely in Southeast Asia. These populations exhibit about 5 % of Denisovan DNA (Reich et al. 2010, 2011). Perhaps – but this is still a hypothesis – the Dali-Maba-Jinniushan group could belong to this archaic Denisovan lineage that lived in wide parts of East Asia.

Further relevant evidence contradicting the idea of regional evolution in China comes from the earliest modern humans of the area. For a long time, the specimens from the Upper Cave at Zhoukoudian and from Liujiang in southern China were regarded to be among the earliest moderns, probably dating to ca. 25–30 Kyr bp

(Hedges et al. 1995; Etler 1996). Due to more recent Uranium-series dates, Shen et al. (2002) have argued that the Liujiang specimen could be much older (>60 Ka or ~100 Ka), but there remain basic uncertainties as to the stratigraphic position of the human remains and thus to their age (Demeter et al. 2012; Keates 2010). In spite of some deviations from present-day Chinese population samples (Howells 1995; Stringer 1999), a multivariate analysis of these early modern Chinese crania (Bräuer and Mímisson 2004) demonstrated that the Upper Cave 101 specimen exhibits the closest affinities with Upper Paleolithic Europeans and also Australians and recent Europeans. For the Liujiang cranium (Fig. 5), the greatest similarity was found with recent North Africans and Europeans as well as with Upper Paleolithic Europeans, terminal Pleistocene North Africans, and sub-Saharan Africans. These similarities appear to support a more recent date for Liujiang. Yet, even if this fully modern specimen would indeed be about 100 Kyr old, it would still clearly contradict any regional evolution from the archaic Dali-Maba-Jinniushan group.

The discussion on the date of the earliest presence of modern humans in East Asia continues, since more human remains have been reported to date between >40 and 100 Ka. These comprise an anterior mandibular fragment from Zhirendong, South China, dated to about 100 Ka (Liu et al. 2010), and a partial adult cranium from the Tam Pa Ling, a cave in Laos, with an age of ca. 46 Ka (Demeter et al. 2012). Because of extant uncertainties on the dating of Liujiang and the fully modern condition of Zhirendong, Demeter et al. (2012) regard the rather well-preserved specimen from Laos as the earliest definitively modern fossil in East Asia. Yet, even with this specimen some questions on the dating and stratigraphy exist (Pierret et al. 2012).

Regarding Australasia, the central assumptions of the multiregionalists have also proven to be no longer tenable. In spite of the huge gap in time between the only *H. erectus* specimen with a well-preserved face, Sangiran 17, and the earliest Australians, Wolpoff et al. (1984, p. 443) saw, especially in the face, a number of continuity features such as the marked prognathism, the maintenance of large posterior dentitions throughout the Middle and Late Pleistocene, an eversion of the lower border of the malar, the persistence of a zygomaxillary ridge, and rounding of the inferolateral border of the orbit. Yet the assumption of interregional gene flow as emphasized by multiregionalists would make it very unlikely that such combinations of features could have been maintained over a period of more than 1 Myr and during the claimed transformation process from the massive facial morphology of *H. erectus* toward that of modern humans (Nei 1998). In addition, Aziz et al. (1996) demonstrated that the earlier reconstruction of the Sangiran 17 cranium done by Wolpoff (Thorne and Wolpoff 1981) is incorrect in several respects. In the revised reconstruction (Fig. 6), the degree of facial prognathism is not marked, but only moderate, and there is no eversion of the lower border of the zygomatic bone, which as a whole bulges laterally. Moreover, the zygomaxillary ridge could not be detected by Aziz et al. (1996, p. 20), nor by myself, on the

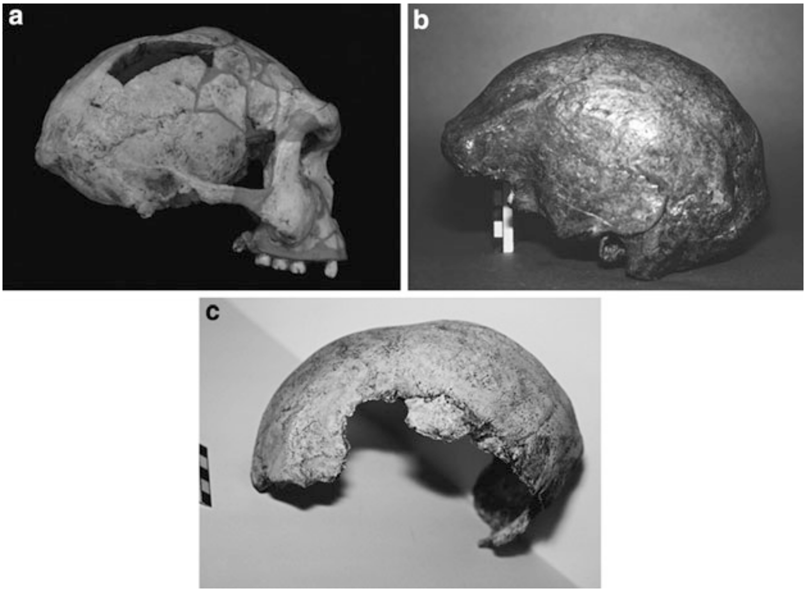


Fig. 6 *Homo erectus* from Indonesia and an early modern Australian: (**a**) Revised reconstruction of Sangiran 17 by Aziz et al. 1996 (Photo: F. Aziz/H. Baba); (**b**) Ngandong; (**c**) Lake Mungo 3

original. There is also no rounding of the inferolateral border of the orbit (Baba et al. 2000, p. 61). Finally, Baba et al. (2000, p. 62) demonstrated that "it does not make sense to compare the degree of facial and dental reduction between Sangiran 17 and Australians, because masticatory adaptation pattern is completely different from each other." Thus, relevant continuity features which have been said to be present on Sangiran 17, dated to ca. 1.3 Ma (Antón 2003), are simply not there or are the result of incorrect reconstruction. Also, in her comprehensive analysis of 20 assumed Australasian cranial features, Lahr (1994) arrived at the conclusion that most of the traits did not show the pattern proposed by the Multiregional Evolution model and quite a number of them occur with high frequency in a robust terminal Pleistocene sample from North Africa, thereby supporting a functional interpretation of these traits.

Detailed analyses of the cranial morphology of Indonesian *H. erectus* show a continuous gradual evolution from the early Pleistocene specimens to the late *H. erectus* from Ngandong (Fig. 6) and Sambungmacan, but no further evolutionary continuity to early modern Australasians (Kaifu et al. 2008). Until recently, the ages of Ngandong and of Sambungmacan, which have long been controversial, ranged between a few hundreds of thousands of years (e.g., Bartstra et al. 1988) to only 30–50 Ka (Swisher et al. 1996). New redating by Ar/Ar and ESR/U-series also arrived at divergent results that nevertheless narrow the age of the Ngandong hominins to between 140 and 540 Ka (Indriati et al. 2011). Thus, it now seems that the Ngandong *erectus* is older than 100 Ka and not contemporaneous with the earliest Australians, such as the fully modern skeleton Lake Mungo 3, southern Australia (Fig. 6), for which several dating approaches have yielded an age of more than 40 Kyr bp and perhaps even up to 60 Kyr bp (Thorne et al. 1999; Bowler and Magee 2000).

Although no conclusive indications for a regional evolution from *H. erectus* to modern Australians appear to exist, the human fossil and subfossil material from Australia as a whole exhibits considerable variability with regard to robusticity. Among these anatomically modern humans, there are very robust as well as gracile specimens as, for example, present in the Kow Swamp material which dates to ca. 22–19 Kyr bp or somewhat more recent (Bräuer 1989; Stone and Cupper 2003). One of the most robust crania is WLH-50 from the Willandra Lakes, which has been absolutely dated to 14 Kyr bp (Simpson and Grün 1998). The cranial vault of this specimen has also been modified by severe pathological alterations (Webb 1990). Notwithstanding the young age and pathology of WLH-50, Wolpoff et al. (2001) chose this cranium instead of the much more appropriate one from Lake Mungo in order to demonstrate regional evolution in Australasia. However, their approach also suffers from fundamental problems with the characteristics used as well as their assessments (Bräuer et al. 2004b). Robust specimens also date from the early Holocene. Possible explanations for the great range of variation might be drift effects in the course of the occupation of the continent but may also include adaptation to an increasingly arid environment toward the peak of the last glacial period (Klein 1999; Baba et al. 2000). As the recent genome sequencing showed, populations of Australia and New Guinea not only exhibit up to 5 % of their DNA from the archaic Denisovans but also 1–4 % of Neanderthal DNA (Reich et al. 2011). Yet, in view of the fact that the earliest fully moderns in Australia are rather gracile, it remains controversial whether this archaic DNA component also contributed to the greater robusticity among the later terminal Pleistocene Australians.

Conclusions

Over the last two and a half decades, the accumulating fossil and molecular evidence has strongly supported the "Out-of-Africa and hybridization" model. Claims by multiregionalists for a larger contribution of Neanderthals to the early modern Europeans cannot be supported by the current evidence. Instead, the most likely scenario appears to be a replacement of the Neanderthals accompanied by only a small amount of gene flow. For the Far East, it is more difficult to examine possible indications of interbreeding since the fossil record of the replacement period is rather poor. Nevertheless, in view of the serious problems regarding the claimed continuity features for China and Australasia and the fact that the earliest modern humans in both areas are fully anatomically modern and do not fit into the concept of regional evolution, no convincing evidence can be seen for long-term regional evolution up to modern humans.

The anatomical modernization process in Africa now appears to be well established by quite a number of diagnostic and reliably dated hominid specimens. To describe the obvious morphological changes of this continuously evolving lineage, three grades or groups of *H. sapiens* have been suggested. This evolutionary sequence led to an early emergence of anatomically modern humans nearly 200 Ka. In view of the obvious continuity from archaics to early moderns and the near-modern morphology of the premoderns, it appears unlikely that anatomically modern humans differ from their direct ancestors on the species level (Stringer 2002a; Bräuer 2008). Instead, during the major part of the Middle Pleistocene, the African fossil record documents a diachronic increase of more derived modern-like conditions. Therefore, it appears adequate to assign the post-*H. erectus* humans to one biological species *H. sapiens* (Klein 2009; Hofreiter 2011). This view is also supported by the fact that the Preneanderthal/Neanderthal lineage which goes back to around 500 Ka bp cannot reasonably be split into different species. It might thus be in agreement with the current evidence (Fig. 7) from Africa and Europe to only assume a speciation between *H. erectus* and (archaic) *H. sapiens* at around 700 or 800 Ka in Africa. Later, early archaic *sapiens* populations spread into Europe evolving toward the Neanderthals. Regarding China, it appears likely that the late Middle Pleistocene humans derived from an eastward dispersal of archaic *H. sapiens* populations, possibly representing the Denisovan lineage, although some regional gene flow from *H. erectus* cannot be excluded as well.

As discussed in this and other chapters, various alternative phylogenetic scenarios have been suggested to describe Middle and Late Pleistocene human evolution. *H. sapiens* is often restricted to modern humans, and its ancestral group (largely equivalent to late archaic *H. sapiens*) has been assigned either to the same species (Stringer 2002a) or to a separate species, *H. helmei* (McBrearty and Brooks 2000). Alternatively, *H. helmei* is regarded as ancestral not only to modern *H. sapiens* but also to *H. neanderthalensis* (Foley and Lahr 1997). These various possibilities, however, have their own problems. For example, the latter phylogeny does not consider that Neanderthal features had long existed in Europe prior to the hypothesized appearance of *H. helmei*. Moreover, suggesting several species within the continuously evolving lineages of later human evolution causes problems in delimiting the taxonomic units (Foley 2001). Such units are rather arbitrarily defined entities without any clear relation to biological species. Studies on extant primates led Jolly (2003, p. 662) to conclude that Neanderthals, Afro-Arabian "premodern" populations, and modern humans are, roughly speaking, biological subspecies, comparable to interfertile allopatric taxa or phylogenetic species of baboons. Thus, it appears well supported from different lines of evidence, including the recent results from nuclear DNA sequencing for widespread archaic-modern hybridization, to regard the European Preneanderthals/Neanderthals and the African Middle Pleistocene lineage to modern humans and the late archaic group in China as belonging to one polytypic species *H. sapiens*. "Speciation remains the special case, the less frequent and more elusive phenomenon, often arising by default" (Grubb 1999, p. 164).

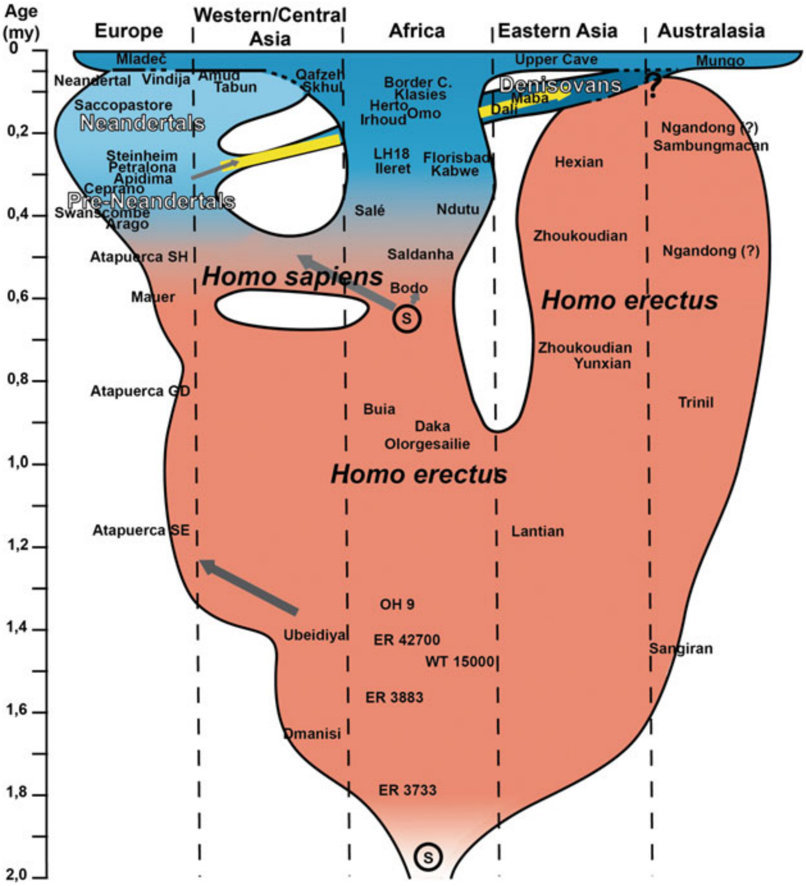


Fig. 7 Origin and evolution of *Homo sapiens*

Cross-References

- ▶ Defining *Homo erectus*
- ▶ Defining the Genus *Homo*
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Later Middle Pleistocene *Homo*
- ▶ Neanderthals and Their Contemporaries
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Population Biology and Population Genetics of Pleistocene Hominins
- ▶ Species Concepts and Speciation: Facts and Fantasies

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Population Biology and Population Genetics of Pleistocene Hominins

Alan R. Templeton

Contents

Abstract

The population genetics of Pleistocene hominins is deduced from three types of data: coalescent processes and haplotype trees estimated from surveys of genetic variation in present-day human populations, ancient DNA extracted from fossils, and overlays of current quantitative genetic variance/covariance matrices upon hominin fossils. The haplotype trees are subjected to nested clade phylogeographic analyses. These analyses show that there were three major expansion events of hominins out of Africa during the last 2 Myr. The first expansion event marked the original dispersal of *Homo erectus* out of Africa into Eurasia. The quantitative genetic analysis of hominin fossils indicates that there was relaxed selection upon at least some morphological features at this time,

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A.R. Templeton (✉)
Department of Biology, Washington University in St. Louis, St. Louis, MO, USA

Department of Evolutionary and Environmental Biology, University of Haifa, Haifa, Israel
e-mail: temple_a@wustl.edu

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perhaps due to an increased use of cultural inheritance in dealing with the environment. Coalescent analyses indicate that the colonization of Eurasia was marked by strong selection at many loci, so although morphological selection may have been relaxed, adaptive processes were still proceeding as humans colonized this new geographical area. A second expansion out of Africa was marked by the spread of the Acheulean culture, implying that the spread of this culture was due to a spread of peoples and not just ideas. The expanding Acheulean populations interbred with existing Eurasian populations, and recurrent gene flow between Eurasian and African populations was established although restricted by isolation by distance after the Acheulean expansion. A third expansion out of Africa marked the spread of many anatomically modern traits that had earlier appeared in Africa. This expansion was also marked by interbreeding, so regional continuity persisted for some traits. Total replacement of Eurasian populations is rejected with a $p < 10^{-17}$, under nested clade phylogeographic analysis, and this strong conclusion has been confirmed by subsequent phylogeographic analysis using Approximate Bayesian Computation after correcting for some statistical errors. Direct studies on ancient DNA also support limited admixture rather than total replacement. Coalescent studies are inconclusive and contradictory both about the size of hominin populations before this last out-of-Africa expansion and the degree of population growth during the expansion phase. Because of admixture and gene flow, humanity evolved into its modern form as a single evolutionary lineage but with geographical differentiation at any given time due to isolation by distance and local adaptation.

Introduction

Population genetics is concerned with the origin, amount, and distribution of genetic variability present in populations of organisms and the fate of this variability through space and time. Variation in genes through space and time constitutes the fundamental basis of evolutionary change, so population genetics can be thought of as the science of the mechanisms responsible for evolution within a species or within a continuous lineage of species through time. The fate of genes through space and time is strongly influenced by a population's demography, so genetic studies can also be used as a powerful tool to investigate past demography.

Most population genetic studies of natural populations involve surveying a sample of individuals from one or more demes (local subpopulations), followed by analyses to infer population structure, demography, and/or the impact of various evolutionary forces such as genetic drift, gene flow, and natural selection. But how does one study the genetics and demography of populations from the distant past, such as hominin populations from the Pleistocene? The most common approach to the study of past populations arises from the subdiscipline of population genetics known as coalescent theory. Because DNA can replicate and pass on copies of itself to the next generation, contemporary DNA contains information from past generations. One can therefore genetically survey contemporary populations and then use phylogenetic techniques to estimate the pattern of past DNA replication events. A DNA replication event produces two copies of DNA from one ancestral molecule, so when looked at backward in time, a DNA replication event corresponds to two molecules of DNA coalescing into a single ancestral molecule. Our ability to infer coalescent events with phylogenetic methods depends on the descendant DNA lineages being distinguishable from one another, so the only coalescent events that can be inferred are those that are also associated with a mutation in one of the DNA lineages.

The distinguishable DNA lineages are called haplotypes, and we can only reconstruct the haplotype tree of a DNA region, that is, the pattern of coalescent events marked by mutational changes. Thus, the rate of mutation in a DNA region places a limit on our ability to infer the evolutionary history of that region. Because of the Mendelian properties of genetic recombination and assortment and because different DNA regions can display different patterns of inheritance (e.g., the DNA on the Y chromosome is paternally inherited but autosomal DNA is inherited through both sexes), different regions of DNA can have different evolutionary histories and can be influenced by different subsets of past demographic events and processes. Moreover, population genetic inference requires genetic variation, so once all the contemporary copies of a gene or DNA region have coalesced back to a single ancestral molecule of DNA, all population genetic information is lost. Because different DNA regions can coalesce to their common ancestral molecule at different times in the past, different genes are informative of different time periods in the past. Natural selection can also affect the coalescent dynamics of a particular gene region, either by increasing the frequency and geographical range of a new, favored haplotype, by maintaining locally adaptive haplotypes, or favoring the maintenance of multiple DNA lineages. In this case, the haplotype tree does not just reflect the impact of past demography, but also past and ongoing natural selection. Populations generally contain much variation in their gene pools. Hence, when a population splits into two or more isolates, those isolates at first share much of their genetic variation. As time proceeds, genetic drift insures that some DNA lineages are lost, and one will eventually become the common ancestral form for a particular isolate. Because of the randomness of genetic drift, this process of DNA lineage sorting can sometimes produce haplotype trees with different topologies than the evolutionary tree of population splits. Finally, populations can differentiate under restricted gene flow, never experiencing true splits followed by isolation. Indeed, if gene flow is sufficiently strong, the entire species may represent a single panmictic population. In these cases there is no evolutionary tree of populations at all, but there are still haplotype trees for specific regions of the genome. For all of these reasons, any one gene or DNA region captures only a portion of a population’s evolutionary history, and the haplotype tree of a gene or DNA region should *never* be equated to the evolutionary history of populations. Many different haplotype trees are required to overcome these difficulties in order to yield a reconstruction of population history. Fortunately, such multi-locus, coalescent analyses are now feasible.

The coalescent approach starts in the present and looks into the past. An opposite approach is to start in the past with some set of assumed conditions and then project into the present using a detailed evolutionary model. This projection is typically accomplished through computer simulation. The parameter space of the assumed model is explored to find the set of parameters that best fits the current genetic observations. Often qualitatively different models are also simulated to find the model that best fits the current genetic observations. This approach does not require haplotype trees, but rather can be applied to wide variety of genetic data sets.

One limitation of both the coalescent and simulation approaches is not easily overcome. Both types of analyses are based upon current genetic variation and therefore are limited to inferences on past populations or subpopulations that have left genetic descendants in present-day populations. Any population that left no descendants is outside the domain of coalescent analyses. DNA from fossils can overcome this limitation, so ancient DNA studies can extend coalescent and simulation analyses. But because evolution is a population process, accurate evolutionary inferences often depend upon having large sample sizes, and the number of fossils that retain useful DNA severely limits ancient DNA approaches. As a result, ancient DNA surveys usually involve limited sample sizes, even when fossils from diverse geographical locations and separated by tens of thousands of years are pooled together as a single "population." Extremely small sample sizes often preclude precise population genetic inference. However, some population genetic inferences depend more on the number of genes sampled than the number of individuals, and since ancient DNA studies on hominins can now span the entire genome, some types of inferences can be made with a high degree of confidence. Hence, ancient DNA studies can now address at least some of the questions addressed by studies based on current variation. This allows a direct cross-validation between the present and the past.

Coalescent approaches and patterns found in current genetic variation can also be used to infer the presence and type of natural selection operating upon specific genes. Hence, some aspects of adaptive evolution in hominin populations can be addressed from surveys of present-day genetic variation. Additional adaptive insights can be achieved by combining genetic surveys on living populations with ancient genomes from fossils. Another approach to studying past adaptive evolution is to use genetic studies on morphological variation in present-day populations to model the evolutionary forces that created morphological change in the fossil record. All four approaches – coalescence of haplotypes, ancient DNA, simulation, and quantitative genetics – will be considered in this chapter with respect to two major aspects of hominin evolutionary history: (1) hominin population structure and historical demographic events and (2) natural selection and adaptive evolution in past hominin populations.

Hominin Population Structure and Historical Demographic Events

Nested Clade Phylogeographic Analyses

Nested clade phylogeographic analysis (NCPA) is a coalescent-based approach to extract information from haplotype trees to infer the qualitative nature of past population structure (patterns of gene flow among geographical areas) and historical demographic events (population range expansions, colonization events, and fragmentation events) (Templeton et al. 1995). NCPA first defines a series of hierarchically nested clades (branches within branches) from the haplotype tree using a set of explicit nesting rules (Templeton et al. 1987; Templeton and Sing 1993). Most human haplotype trees are rooted, so the oldest clade is known in any given nested category. The relative temporal orderings are used to analyze the spread of haplotypes and clades through space and time. NCPA next quantifies the spatial distribution of haplotypes and clades by measuring how widespread a clade is spatially and how far away a clade is located from those clades with which it is nested into a higher-level clade (Templeton et al. 1995). To adjust for sampling, the nested clade analysis uses a random permutation procedure to test the null hypothesis that the clades nested within a higher-level clade have no geographical associations. Because the nested clades are asymptotically independent (Templeton et al. 1995), the Bonferroni procedure is used to correct for multiple testing. All subsequent inferences are limited to those clades associated with a statistically significant rejection of the null hypothesis of no geographical association.

Statistical significance tells us that geographical associations exist within the haplotype tree, but they do not tell us how to interpret those geographical associations. Indeed, no single test statistic discriminates between recurrent gene flow, past fragmentation, and past range expansion in NCPA. Rather, it is a pattern formed from several statistics that allows discrimination. Also, many different patterns can sometimes lead to the same biological conclusion, and sometimes a statistically significant pattern has no clear biological meaning because of inadequate geographical sampling or a lack of genetic resolution. Finally, NCPA searches out multiple, overlaying patterns within the same data set. In light of these complexities (which reflect the reality of evolutionary possibilities and sampling constraints), an inference key was provided as an appendix to Templeton et al. (1995), with the latest version being available at http://darwin.uvigo.es/ along with the program GEODIS for implementing the nested clade analysis.

Although NCPA has many strengths, it does have limitations. In particular, inference is limited by (1) sample size and sample sites, (2) insufficient genetic resolution to detect an event or process that actually occurred, and (3) false inferences arising from the evolutionary stochasticity of the coalescent process or by the haplotype tree being skewed or otherwise altered by natural selection. In light of these limitations, the inference key has been extensively validated by applying NCPA to actual data sets with 150 a priori expectations (Templeton 2004b). The inference key did well, with the most common error being the failure to detect a known event. Only rarely did NCPA result in a false positive. The failure to detect known events was due to the fact that an appropriate mutation had not occurred in the right place and time to mark the event. This shows that no one locus or DNA region can capture the totality of a species' population structure and evolutionary history. Concerning false positives, the processes of mutation and genetic drift, which shape the haplotype tree upon which the NCPA is based, are both random processes. Therefore, the expected pattern for a particular event or process can sometimes arise by chance alone, leading to a false biological inference. Moreover, natural selection can lead to false biological inferences by skewing the shape of the haplotype tree and the geographical distribution of certain haplotypes.

The occurrence of false negatives and false positives can be reduced by performing NCPA upon many loci or gene regions (Templeton 2002). Using multiple DNA regions reduces the danger of missing an event or process due to the lack of an appropriately placed mutation in time and space for any one DNA region. The chance of making a false inference is reduced by cross-validating inferences across DNA regions. Templeton (2002) used a multi-locus NCPA based on the human mitochondrial genome and nine nuclear genome regions to infer recent human evolutionary history. What was most remarkable about the cross-validated inferences in this case was the incompleteness found in any one DNA region. This illustrates that failure to detect events or processes with a single DNA region is a common phenomenon. Interestingly, most inferences that were made with one gene were cross-validated by other DNA regions, thereby indicating that false positive inferences are rare in NCPA. This is the same pattern observed when validating the inference key with real data with a priori expectations (Templeton 2004b).

The power and low false positive rate of multi-locus NCPA was confirmed by the simulations of Knowles and Maddison (2002). Knowles and Maddison simulated an evolutionary history of micro-vicariance, in which each local population was a genetic isolate due to past fragmentation events. Moreover, the time between population splits was less than the expected coalescent times and the population sizes were large, thereby insuring the sharing of much ancestral polymorphism across isolates. This is a difficult inference problem, and indeed their own simulation procedures fared poorly (Knowles and Maddison 2002). Although the multi-locus version of NCPA had been published 9 months earlier (Templeton 2002), Knowles and Maddison chose to apply only the 1998 single-locus version of NCPA to their simulated data, despite the fact that micro-vicariance had been explicitly excluded from the single-locus version (Templeton et al. 1995). Accordingly, it is not surprising that single-locus NCPA fared poorly when used to analyze these simulated data sets. However, when the 2002 version of multi-locus NCPA was applied to these same simulated data sets, a 100 % accurate reconstruction of the population's evolutionary history was made with no false inferences (Templeton 2009a). These simulations therefore demonstrate the power of multi-locus NCPA to reconstruct difficult evolutionary histories even when no single locus could yield accurate inferences and the low false positive rate of multi-locus NCPA.

Cross-validation in Templeton (2002) was based upon concordance across DNA regions of NCPA inferences by type and geographical location. Assessing concordance of inference type and locality is straightforward as these are categorical variables, but inferences should also be temporally concordant. Estimated times of events are quantitative variables with considerable error due to the high stochasticity associated with the coalescent process (Templeton 2004b). Therefore, Templeton (2004a) developed log-likelihood ratio tests of temporal concordance. Panchal and Beaumont (2010) performed simulations to determine the false positive rates under a variety of scenarios using this triple cross-validation of inference type, geographical location, and a formal statistical test of temporal concordance. In general, they found low rates of false positives that were below the nominal rate of 5 %. The one exception was for inferences involving gene flow. Panchal and Beaumont claimed that gene flow inference is subject to a high false positive rate "because there is no stipulation that the inferences should be concordant across time" (Panchal and Beaumont 2010, p. 418). This claim is false. Gene flow is a recurrent event, so temporal concordance does not mean that all gene flow inferences must have occurred at exactly the same time. Therefore, likelihood ratio tests were designed for temporal concordance across a *time interval* for gene flow (Templeton 2004a, Eq. 12; Templeton 2009b, Eq. 2). The 2009 test specifically tests the null hypothesis of no gene flow between two areas in a specific time interval. Panchal and Beaumont (2010) are correct in concluding that their reported high false positive rate for gene flow inferences was due to *their* failure to test for temporal concordance, but Panchal and Beaumont made an egregious misrepresentation of NCPA by claiming that such a test did not exist. Whenever Panchal and Beaumont actually implemented multi-locus NCPA, the false positive rates were always below the nominal rate. These simulations therefore demonstrate that multi-locus NCPA is a powerful and accurate method for reconstructing past evolutionary histories from current genetic data.

Because multi-locus NCPA uses haplotype trees, only those gene regions that have little to no recombination can be used. Recombination can place together in a single DNA molecule different segments that may have had different evolutionary histories, thereby undermining the very idea of an evolutionary tree of haplotypes. This is why the initial studies using NCPA for human evolution were limited to the nonrecombining molecules of mitochondrial DNA (mtDNA) and the Y chromosome (Y-DNA). However, recombination in the human genome is not evenly distributed, but rather is concentrated into hotspots with little to no recombination in many of the regions bounded by hotspots (Templeton et al. 2000a). Hence, with modern genomics it is not difficult to find many regions in the human genome that are amenable to multi-locus NCPA. These nonrecombining regions are the ones upon which human evolutionary history is most clearly and cleanly written.

Multi-locus NCPA was first applied to infer recent human evolution with 10 gene regions (mitochondrial DNA, Y chromosomal DNA, and 8 nuclear gene regions) (Templeton 2002) and was later expanded to include 15 additional nuclear gene regions (Templeton 2005, 2008). The *MX1* data used in Templeton (2002) was later

Table 1 The times to the most recent common ancestor (TMRCA) in millions of years ago for the 24 loci subjected to NCPA

Gene region	TMRCA
Y-DNA	0.23
mtDNA	0.24
MAO	0.449
FIX	0.47
MSN/ALAS2	0.656
Xq13.3	0.67
G6PD	0.692
HS571B2	0.71
APLX	0.84
MC1R	0.85
ECP	1.09
EDN	1.15
AMELX	1.178
MS205	1.25
HFE	1.27
TNFSF5	1.34
Hb-Beta	1.63
CYP1A2	1.69
RRM2P4	1.714
PDHA1	1.91
FUT6	1.9375
Lactase	2.14
CCR5	2.52
FUT2	5.04

found to contain some paralogous copies, so it was subsequently excluded, leaving a total of 24 gene regions. Interestingly, the inferences from *MX1* had already been excluded from the earlier analysis on the basis of the cross-validation procedure (Templeton 2005, 2008). Coalescent theory predicts that there will be a large variance in coalescent times to the most recent common ancestor (TMRCA) among the various gene regions, with the unisexual, haploid regions (mtDNA and Y-DNA) having an expected coalescence time of N_{ef} generations (the long-term inbreeding effective size of humanity), the X-linked loci having an expected coalescence time of $3N_{\mathrm{ef}}$, and the autosomal loci having an expected coalescence time of $4N_{\mathrm{ef}}$ (Templeton 2002). Table 1 gives the TMRCAs for the 24 loci used in this analysis. The average coalescence times do indeed fit the expected ranking, and there is also the large expected variance within each category. Table 1 further shows that there is a rather continuous temporal coverage up to about 2.5 Ma. Thus, with these 24 loci, events going back to around 2 Ma can be inferred with potential cross-validation, which represents a significant improvement in the informative temporal range over that of the original 10 loci (Templeton 2002).

Table 2 The NCPA inferences and their estimated times (in Ma) from the 24 gene regions that yielded significant and interpretable results. Time is indicated only as "recent" for events too young to be reliably dated by phylogenetic means. Only gene flow inferences between Africa and Eurasia are shown

Gene region	Range expansion events	Restricted gene flow between Africa and Eurasia
mtDNA	Out of Africa, $t = 0.1308$	Isolation by distance, recent
	To N. Eurasia, recent	
	To Siberia, recent	
	To the Americas followed by fragmentation, recent	Isolation by distance, recent
	Within the Americas, recent	
Y-DNA	Out of Africa, $t = 0.0916$	Isolation by distance, recent
	Out of Asia to Europe and Africa, recent	Isolation by distance, recent
CCR5	–	Isolation by distance, $t = 1.9844$
CYP1A2	Out of Africa, $t = 1.43$	Isolation by distance, $t = 0.2649$
		Isolation by distance, $t = 0.3532$
ECP	–	Isolation by distance, $t = 0.5824$
EDN	To the Americas, recent	Isolation by distance, $t = 0.6912$
FIX	–	Isolation by distance, $t = 0.3378$
FUT2	Out of Africa, $t = 2.686$	With some long-distance dispersal, recent
		Isolation by distance, $t = 0.9948$
		Isolation by distance, $t = 1.5917$
FUT6	Out of Africa, $\mathrm{t} = 0.5$	With some long-distance dispersal, recent
		Isolation by distance, $t = 1.25$
		Isolation by distance, $t = 1.3$
G6PD	To the Americas, recent	Isolation by distance, $t = 0.4808$
	Africa and Eurasia, origin ambiguous, $t = 0.625$	
Hb-β	Out of Africa, $t = 0.8212$	Isolation by distance, $t = 0.4927$
	Out of Asia to Europe and Africa, recent	
HFE	Out of Africa, $t = 0.169$	Isolation by distance, $t = 0.169$
	Within Eurasia, $t = 0.2535$	Isolation by distance, $t = 0.3944$
	Out of Africa, $t = 0.5493$	
HS571B2	Out of Africa, $t = 0.1558$	–
Lactase	Out of Africa, $t = 0.86$	Isolation by distance, recent
	Africa and Eurasia, origin ambiguous, $t = 1.93$	
MC1R	Out of Africa, $t = 1.00$	–
	To N. Eurasia, recent	
MS205	Africa and Eurasia, origin ambiguous, $t = 1.87$	Isolation by distance, recent
	To the Americas, recent	
	To the Pacific, recent	
	To the Pacific, recent	

(*continued*)

Table 2 (continued)

Gene region	Range expansion events	Restricted gene flow between Africa and Eurasia
MSN/ ALAS2	–	Isolation by distance, $t = 0.164$
PDHA1	–	Isolation by distance, $t = 0.8597$
RRM2P4	Out of Africa, $t = 0.14$	With some long-distance dispersal, $t = 0.6$
TNFSF5	To the Americas, recent	–
Xq13.3	–	Isolation by distance, $t = 0.48$

Table 2 shows the inferences made from the 24 gene regions along with their estimated times of occurrence. Some events could not be timed because there were too few or no mutations available to obtain a reliable estimate. The inferences shown in Table 2 span most of the Pleistocene.

Table 2 reveals 15 different identifications of out-of-Africa range expansion events or Africa/Eurasian range expansion events of ambiguous origin. These 15 events are concordant by type (range expansion) and geographical location (expansion events involving both African and Eurasian populations, and when geographical resolution of the origin is possible, it is always out of Africa). To test temporal concordance of these 15 inferences, their estimated times are regarded as random variables with a mean given by a standard phylogenetic estimator (Takahata et al. 2001) of the age of the youngest clade contributing in a statistically significant fashion to the inference, with a calibration point of 6 Ma for the divergence between humans and chimpanzees (Templeton 2004a). The variance of this time is given by Tajima (1983).

$$\sigma^2 = \frac{T^2}{(1 + k)} \tag{1}$$

where T is the standard phylogenetic estimator of age and k is the pairwise divergence among present-day haplotypes as measured by the number of mutations that have accumulated in the descendants of the haplotype or node whose age is estimated to be T. Equation 1 incorporates two sources of error into the variance associated with estimator T. First, the numerator of Eq. 1 is T^2, reflecting the evolutionary stochasticity of the coalescent process itself in which the variance is proportional to the square of the mean (Donnelly and Tavare 1995; Hudson 1990). The other factor that influences the variance is k, which depends upon the number of mutations that have accumulated in the DNA lineages from T to the present. This can vary considerably from locus to locus, depending upon the local substitution rates and upon the amount of DNA being sequenced. Because k is generally very small for recent events, phylogenetic dating procedures are often unreliable for recent events (Rannala and Bertorelle 2001).

If the population under study has not been significantly fragmented into subpopulations and evolution is neutral, then the distribution of t_i, the time of a phylogeographic event or process inferred from DNA region i, can be approximated by a gamma distribution (Kimura 1970):

$$f(t_i|T_i, k_i) = \frac{t_i^{k_i} e^{-t_i(1+k_i)/T_i}}{\left(\frac{T_i}{1+k_i}\right)^{1+k_i} \Gamma(1+k_i)} \tag{2}$$

where k_i is the average pairwise nucleotide diversity among the haplotypes in DNA region i in the youngest monophyletic clade that contributed in a statistically significant fashion to the NCPA inference of interest, and T_i is the age obtained by the phylogenetic estimator (Templeton 2004a). Given that the NCPA did not reveal any cross-validated fragmentation events except perhaps very early in the Pleistocene between Africa and Eurasia (the exclusive focus of this chapter) that were subsequently mostly erased by range expansions and admixture, the gamma distribution assumption is justified for the human data.

Templeton (2004a) used these gamma distributions to derive maximum-likelihood estimators of the time of an event based on multi-locus data and to derive a log-likelihood ratio test of the null hypothesis that n separate inferences of a geographically concordant event are also temporally concordant; that is, they are the same event. Figure 1 shows the gamma distributions for the 15 inferences of range expansion involving African and Eurasian populations. The log-likelihood ratio test rejects the null hypothesis that all 15 events are temporally concordant with a probability value of 3.89×10^{-15}. Thus, the genetic evidence is overwhelming that there were multiple range expansion events out of Africa during the last 2 Myr (million years) of human evolution. An inspection of Fig. 1 reveals that the time distributions for the 15 events cluster into three distinct groupings. Accordingly, the null hypotheses of temporal concordance within each of these three groupings were tested, and in all cases there was strong concordance within ($p = 0.95$ for the most recent expansion out of Africa, $p = 0.51$ for the middle expansion, and $p = 0.62$ for the oldest expansion). Pooling together the inferences from j homogeneous loci also results in a gamma distribution with mean and variance (Templeton 2004a):

$$\text{Mean} = \hat{T} = \frac{\sum_{i=1}^{j} t_i(1+k_i)}{\sum_{i=1}^{j} (1+k_i)} \tag{3}$$

$$\text{Var}\left(\hat{T}\right) = \frac{\sum_{i=1}^{j} (1+k_i)^2 \text{Var}(t_i)}{\left(\sum_{i=1}^{j} (1+k_i)\right)^2} = \frac{\sum_{i=1}^{j} (1+k_i) t_i{}^2}{\left(\sum_{i=1}^{j} (1+k_i)\right)^2} \tag{4}$$

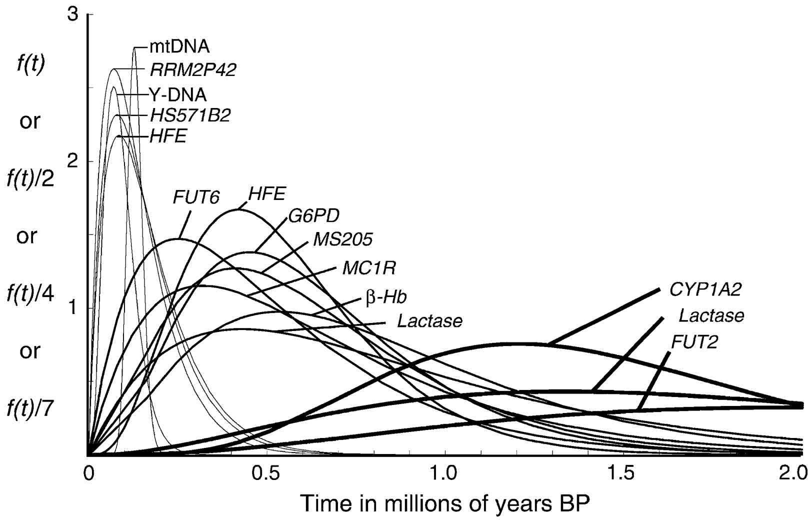

Fig. 1 The distributions for the ages of range expansion events involving Africa and Eurasia, all of which are out-of-Africa events when the geographical origin is unambiguous. The x-axis gives the age in millions of years before present, and the y-axis gives the gamma probability distribution $f(t)$ that was fitted to the data from a particular locus or DNA region. Because the probability mass is so concentrated close to the y-axis for several genes, the gamma distribution was divided by 7 for mtDNA, by 4 for Y-DNA, and by 2 for HFE, HS571B2, and RRM2P4 to yield a better visual presentation. The age distributions fall into three clusters, shown by *thin black lines*, *medium colored lines*, and *thick dashed lines*, respectively

Combining Eq. 1 with Eq. 4, the effective number of informative mutations about the age of the event based on pooled data, k_{eff}, is given by

$$k_{\text{eff}} = \frac{\hat{T}^2}{\text{Var}(\hat{T})} - 1 \tag{5}$$

The standard log-likelihood ratio test given in Templeton (2004a) can be used to test the null hypothesis that two or more times based on pooled data are the same by using Eqs. 3 and 5. The log-likelihood ratio test of temporal homogeneity of the most recent and middle out-of-Africa expansion events yields a chi-square statistic of 40.84 with 1° of freedom with a p-value of 1.66×10^{-10}. Hence, the null hypothesis of temporal concordance is strongly rejected, and the first two clusters shown in Fig. 1 define two distinct out-of-Africa expansion events. The log-likelihood ratio test of homogeneity of the middle and oldest out-of-Africa expansion events also rejects temporal concordance with a chi-square statistic of 8.85 with 1° of freedom and a p-value of 0.0029. Hence, all three clusters shown in Fig. 1 identify separate events that are all cross-validated by multiple loci. The estimated times and 95 % confidence intervals for these three out-of-Africa range expansions are shown in Table 3.

Table 3 The estimated times and 95 % confidence limits of the NCPA inferences of out-of-Africa range expansions when multiple loci are pooled according to the results of log-likelihood ratio tests

Time of expansion (Ma)	More recent age limit	Older age limit
0.1304	0.0965	0.1693
0.6508	0.3917	0.9745
1.9007	0.9937	3.0969

These NCPA inferences from molecular genetic data are consistent with the fossil and archaeological record. The oldest expansion, genetically dated to 1.9 Ma, corresponds well to the fossil dating of the original expansion of *Homo erectus* (which includes *ergaster* in this chapter) from Africa into southern Eurasia at 1.85 Ma (Ferring et al. 2011) and far East Asia by 1.7 Ma (Zhu et al. 2008). Dennell (2003) has argued that these early Pleistocene fossil finds in Eurasia may not have represented permanent settlement but also acknowledges the difficulty of inferring (or rejecting) regional continuity over a long-time period from temporally sporadic fossil and archaeological finds from a single geographical area. Genetics can offer an important tool that complements the fossil and archaeological data. Recall that the NCPA can only detect the genetic signatures of past populations that have made at least some genetic contribution to current populations. This statistically significant signal of an expansion into Eurasia in the late Pliocene to early Pleistocene, cross-validated by three genes, would not exist at all if these initial Eurasian colonies had not left some descendants in present-day Eurasian populations. Hence, the initial colonization of Eurasia by *Homo erectus* was a successful one that resulted in the permanent settlement of at least parts of Eurasia.

The middle expansion out of Africa shown in Table 3 is consistent with the spread of the Acheulean stone-tool culture out of Africa and into Eurasia. Evidence for this culture is found first in Africa at 1.76 Ma (Beyene et al. 2013; Lepre et al. 2011), with the earliest non-African sites being older than 1 Ma (Pappu et al. 2011). However, Acheulean sites are not widespread in Eurasia until about 0.6–0.8 Ma, particularly eastern Asia (Hou et al. 2000). This has led to the suggestion by some that there were two Acheulean expansions out of Africa: the first at about 1.4 Ma and the second at 0.6–0.8 Ma (Aguirre and Carbonell 2001; Bar-Yosef and Belfer-Cohen 2001; Goren-Inbar et al. 2000). As outlined above, the current analysis indicates a statistically significant out-of-Africa expansion at 0.65 Ma (0.3917–0.9745 Ma), which corresponds well with the second, more widespread, Acheulean expansion. However, this genetic analysis does not falsify the hypothesis that there was an earlier Acheulean expansion at 1.4 Ma. Indeed, the out-of-Africa expansion detected by *CYPA2* dates to 1.43 Ma. However, because of the large variances associated with older coalescent-based estimates of age (Eq. 1), this event at 1.43 Ma could not be distinguished from the older out-of-Africa events detected by *FUT2* and *Lactase* with the likelihood ratio tests described above. Thus, there may well have been an Acheulean expansion at 1.4 Ma, but because this event is between the original out-of-Africa expansion by *Homo erectus* and the much stronger (in terms of both archaeological and genetic evidence) Acheulean expansion between 0.6 and 0.8 Ma, it will take a much larger data set to achieve statistical discrimination. Another explanation is that the Acheulean expansion at 1.4 Ma may have been very limited geographically, perhaps confined to the Middle East and southern India. A limited range expansion from Africa would not be detectable by most of the loci analyzed here because of sparse geographical sampling in the Middle East and India. Finally, it is also possible that the 1.4 Ma Acheulean expansion was only a cultural expansion, in which case it would be invisible to NCPA.

It is not clear from the archaeological evidence whether the 0.6–0.8 Ma Acheulean expansion was solely the diffusion of ideas from Africa or also involved movement of populations or individuals (Saragusti and Goren-Inbar 2001). Here, the genetic data can complement the archaeological data. NCPA can only detect movements of reproducing populations and individuals, not ideas. By combining NCPA with archaeology, it is likely that the 0.6–0.8 Ma Acheulean expansion represented a movement of both people and ideas. Another question that cannot be answered by the archaeological data alone is what happened when these Acheulean peoples coming out of Africa encountered the Eurasian populations? Perhaps the Acheulean peoples drove the earlier inhabitants to extinction, completely replacing them. Alternatively, the expanding Acheulean peoples could have interbred with the Eurasian populations. The Acheulean replacement hypothesis can be tested by noting that if complete replacement had occurred, there would be no genetic signatures of events or genetic processes in Eurasia that would be older than this expansion event (Templeton 2004a). This prediction stems from the simple fact that NCPA can only detect events and processes that affected past populations that left genetic descendants in present-day populations. The Acheulean replacement hypothesis can therefore be tested by testing the null hypothesis that the gamma distribution marking the Acheulean expansion has a mean time that is not significantly older than other Eurasian events or processes with older estimated times. To be conservative in the definition of "older," an event or process will only be regarded as older than the Acheulean expansion if its estimated age falls in the older 1 % tail of the pooled gamma distribution that describes the Acheulean expansion. This 1 % cutoff is calculated from the pooled Acheulean gamma distribution to be 1.0476 Ma. NCPA identified four events or processes with estimated times older than 1.0476 Ma: the first out-of-Africa expansion at 1.9 Ma and three inferences of restricted gene flow dating from 1.25 Ma to 1.9844 Ma (Table 2). The log-likelihood ratio test of the null hypothesis that these four other events and processes involving Eurasian populations are no older than the Acheulean expansion yields a chi-square of 10.37 with 4 degrees of freedom, which is significant at the 5 % level ($p = 0.0346$). Hence, the null hypothesis of Acheulean replacement is rejected. The expansion of people from Africa about 0.6–0.8 Ma was therefore marked both by bringing a new culture to and by interbreeding with Eurasian populations.

The Acheulean range expansion from Africa dated to 0.65 Ma (Table 3) is also compatible with the fossil record. After the initial expansion of *Homo erectus* out of

Africa about 1.9 Ma (Table 3), there was little change in average brain size up to 0.7–0.6 Ma, after which cranial capacities show a substantial increase (Lepre et al. 2011; Relethford 2001b; Rightmire 2004; Ruff et al. 1997). Hence the fossil record, the archaeological record, and the genetic analysis presented here all imply that an important transition in human evolution occurred about 0.65 Ma.

The final out-of-Africa expansion is genetically dated to 130,000 years ago (Table 3). Many anatomically modern traits first appeared in sub-Saharan Africa around 200,000 years ago (McDougall et al. 2005), then appeared outside of sub-Saharan Africa in northern Africa, the Arabian Peninsula, and Levant between 130,000 and 125,000 years ago (Armitage et al. 2011; Grun et al. 2005; Vanhaeren et al. 2006), and finally reached far eastern Asia no later than 110,000 years ago (Jin et al. 2009; Liu et al. 2010). Once again, the genetic date from NCPA agrees remarkably well with the fossil and archaeological records.

There has been considerable controversy over whether or not this most recent out-of-Africa expansion event was also a replacement event. This recent replacement hypothesis can be tested in the same manner as the Acheulean replacement hypothesis. The older 1 % tail of the gamma distribution that describes this recent out-of-Africa expansion occurs at 0.1774 Ma. Two older out-of-Africa expansion events occurred, as previously discussed, as well as an expansion event within Eurasia dated to 0.2535 Ma (Table 2). However, this within-Eurasia expansion event is not cross-validated by any other locus, so it will be ignored in this and all subsequent analyses. In addition to the two expansion events, there are 15 inferences of restricted gene flow involving Eurasian populations that have estimated ages older than 0.1774 (Table 2). The log-likelihood ratio test of the null hypothesis that all 17 of these times are no older than the most recent out-of-Africa expansion event yields a chi-square statistic of 118.18 with 17 degrees of freedom, which yields a p-value of less than 10^{-17}. Hence, the genetic data overwhelmingly reject the out-of-Africa replacement hypothesis. There is no doubt from NCPA that this spread of humans with many anatomically modern traits resulted in interbreeding with at least some Eurasian populations.

Several more range expansions were detected by NCPA: expansions within Eurasia, including the colonization(s) of new areas in Northern Eurasia and colonizations of the Pacific and the Americas. These expansions were marked by genetic regions with too few mutations to date, but they were inferred to have occurred after the most recent out-of-Africa expansion. More extensive data on the Y chromosome has allowed the dating of an expansion originating in Eurasia to 41,000–52,000 years ago (Wei et al. 2013). As this expansion was marked by both Y-DNA and nuclear DNA in the NCPA but not mtDNA, even though mtDNA had the best sampling and genetic resolution, this Paleolithic expansion was most likely male-mediated and therefore must have involved interbreeding with previously established populations.

The NCPA results indicate that expansions coupled with interbreeding or admixture were not the only source of genetic contact between African and Eurasian populations during much of the Pleistocene. Figure 2 shows the gamma distributions for all the inferences of restricted gene flow among African and

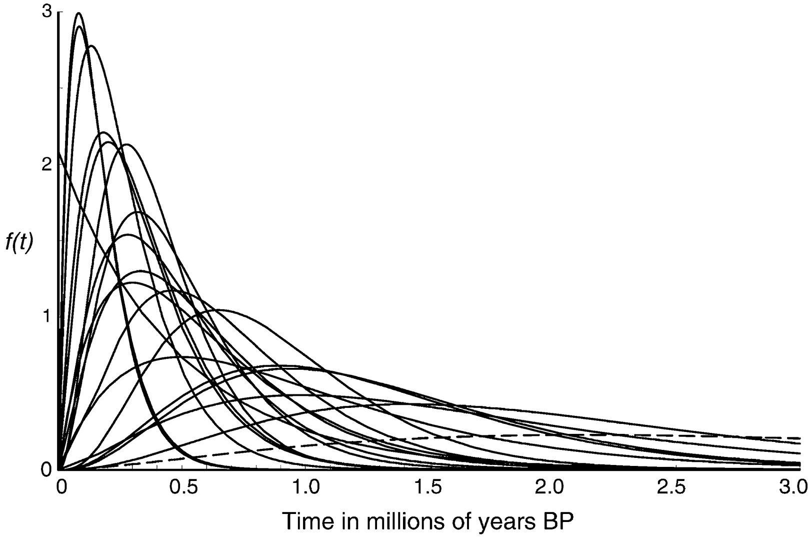

Fig. 2 The distributions for the ages of the youngest clade contributing to a significant inference of restricted gene flow, primarily with isolation by distance. The x-axis gives the age in millions of years before present, and the y-axis gives the gamma probability distribution, $f(t)$. The genes or DNA regions yielding these distributions are, as ordered by their peak values of $f(t)$ going from left to right: Xq13.1, *MSN/ALAS2*, *HFE*, *FIX*, *HFE*, *G6PD*, *βHb ECP*, *RRM2P4*, *EDN*, *PDHA1*, *CYP1A2*, *FUT2*, *FUT6*, *FUT6*, *FUT2*, *CYP1A2*, *CCR5*, and *MX1*. The curve for *MX1* is shown in a *dashed line* to emphasize its outlier status (Templeton 2002). Several other inferences of restricted gene flow that were too recent to date phylogenetically are not shown and not used in the analyses

Eurasian populations from Table 2. Almost all of the older inferences of gene flow indicate that it was restricted by isolation by distance, but some of the more recent inferences (often not datable by phylogenetic techniques) indicate some long-distance dispersal as well. This means that this genetic interchange was mostly due to short-distance movements to neighboring demes (other than the three major population-level expansions), but copies of genes could have spread throughout Africa and Eurasia via gene flow, using local demes as stepping stones to cross vast distances over many generations.

A glance at Fig. 2 versus Fig. 1 reveals a dramatic difference; the inferences of range expansion are clustered, but the inferences of restricted gene flow form a continuum across much of the Pleistocene. The continuum defined by the genes is expected if gene flow restricted by isolation by distance were a recurrent evolutionary force throughout much of the Pleistocene, with no lengthy interruptions.

Because gene flow is a recurrent evolutionary force, there is no expectation of different inferences of restricted gene flow from the various genes to be temporally concordant, in contrast to historical events such as rapid range expansions. But it is possible to test the null hypothesis of isolation (no gene flow) between two areas in the time interval l to u. In particular, if j is the number of loci that yield an inference of gene flow within the time interval l to u between the two areas of interest, the likelihood ratio test (*LRT*) of the null hypothesis of isolation between the two areas in the time interval l to u is

$$LRT\big(\text{isolation in } [l,u] = -2\sum_{i=1}^{j}\ln\left[1-\int_{l}^{u}\frac{t_i^{k_i}e^{-t_i(1+k_i)/T_i}}{\left(\frac{T_i}{1+k_i}\right)^{1+k_i}\Gamma(1+k_i)}dt_i\right] \tag{6}$$

with the degrees of freedom being j (Templeton 2009a).

During the early Pleistocene in the time interval between the first out-of-Africa expansion (1.9 Ma) and the Acheulean expansion (0.65 Ma), there were seven inferences of gene flow with isolation by distance between Africa and Eurasia (Table 2). The likelihood ratio test of the null hypothesis of isolation (no gene flow) between Africa and Eurasia given by Eq. 6 yields a log-likelihood ratio statistic of 11.86 with 7 degrees of freedom, which is not significant at the 5 % level. Hence, after the first expansion of *Homo erectus* into Eurasia, there was no significant gene flow between Eurasian and African populations up to the time of the Acheulean expansion. In the time interval between the Acheulean expansion (0.65 Ma) and the expansion of anatomically modern humans out of Africa (0.13 Ma), there are 11 inferences of gene flow between Africa and Eurasia, with Eq. 6 yielding a log-likelihood ratio statistic of 23.94 with 11 degrees of freedom, which yields a p-value of 0.013. Hence, the null hypothesis of isolation between Africa and Eurasia is rejected during this time interval. Humans by 650,000 years ago had the capability of moving both in and out of Africa and did so on a recurrent basis.

Figure 3 summarizes the cross-validated, statistically significant conclusions from the NCPA based on 24 genes or DNA regions. The inferences in Fig. 3 of ancient and recurrent gene flow punctuated by major population movements out-of-Africa coupled with interbreeding are consistent with the fossil record. Many fossil traits display a pattern of first appearing in Africa and then spreading throughout Eurasia (Stringer 2002), whereas other traits display a pattern of regional continuity (Wolpoff et al. 2000; Wu 2004). These two patterns are often regarded as mutually exclusive alternatives, but they are not under a model of genetically interconnected populations and no total replacement. As long as there is genetic interchange among populations, the Mendelian mechanisms of recombination and assortment allow different traits influenced by different genes to have different evolutionary fates. Some traits could have spread due to the joint actions of gene flow, admixture, and natural selection, whereas other traits may not have spread as rapidly or not at all due to a lack of selection or due to local selective pressures. Recurrent gene flow and admixture therefore provide the genetic interconnections that explain *all* of the fossil trait patterns during this time period, as well as current distributions of genetic variation in humans (Dugoujon et al. 2004; Eller 1999; Eswaran 2002). This model of gene flow and interbreeding also explains why current genetic variation in human populations does not fit an evolutionary tree model in which different human populations are treated as distinct “branches” on an evolutionary tree. Although the

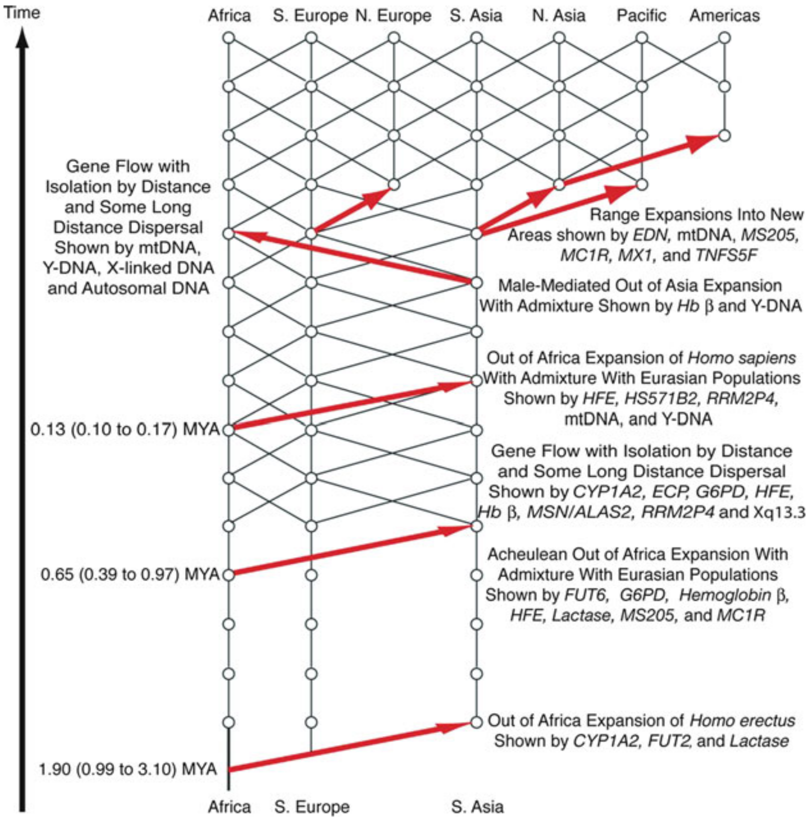

Fig. 3 A model of recent human evolution as inferred from NCPA. All inferences are cross-validated by two or more genes and are statistically significant at least at the 5 % level. Major expansions of human populations are indicated by *arrows*, and the time periods for the out of Africa are the 95 % confidence limits given in Table 3. Genetic descent is indicated by *vertical lines* and gene flow by *diagonal lines*

human evolutionary genetic literature is filled with portrayals of human populations as branches on a tree, none of these population evolutionary trees actually fit the genetic data when tested (Templeton 1998, 2003, 2013). Instead, patterns of genetic differentiation among current human populations fit an isolation-by-distance model much better than a tree model (Eller 1999, 2001; Templeton 1998, 2003, 2013).

Ancient DNA Analyses

The NCPA overwhelmingly indicates that the most recent out-of-Africa range expansion event was not a total replacement event. This does not mean, however, that there was interbreeding with all Eurasian populations. The possibility of some local replacement is compatible with the NCPA, but that possibility is not testable with NCPA because its inference is limited to historical populations that have left some genetic descendants in present-day populations. One way of addressing this possibility is to extract DNA from hominin fossils.

Working with ancient DNA is difficult. Because mtDNA is much more abundant than nuclear DNA, the initial ancient DNA studies focused on mtDNA (Caramelli et al. 2003; Currat and Excoffier 2004; Knight 2003; Krings et al. 2000; Serre et al. 2004). These studies revealed that Neanderthal mtDNA represents a unique mitochondrial lineage that is distinct both from present-day human mtDNA and from the mtDNA found in fossil but anatomically modern specimens from comparable time periods. This pattern has been interpreted to mean that there was no or extremely little interbreeding between Neanderthals and their more anatomically modern contemporaries. However, there are difficulties with these conclusions from ancient DNA studies.

First are the technical difficulties. Ancient DNA is subject to damage over time, and resulting lesions can create artifactual substitutions (Caldararo and Gabow 2000; Hansen et al. 2001). One test for artifactual substitutions makes use of the considerable age range found in the Neanderthal fossils used as sources for DNA. If the apparent divergence is real, then the oldest Neanderthal samples should tend to be closest to current human mtDNA because they are temporally closer to the common ancestral sequence for Neanderthal and modern human mtDNA. In contrast, if DNA damage has made a large contribution to the apparent divergence, then the oldest Neanderthal sequences should be the farthest from that of modern humans. The later pattern is true (Gutierrez et al. 2002). Because the samples are small, one could argue that just by chance the oldest Neanderthal sequences just happened to come from an abnormally highly divergent lineage of Neanderthal mtDNA; but these results indicate that DNA damage cannot be discounted as a significant source of error in these early studies. In addition, ancient DNA extracts induce artifactual mutations, both nucleotide substitutions and insertions/deletions, in a nonrandom fashion such that the same artifacts are independently created in controlled experiments (Pusch and Bachmann 2004). Moreover, many of the sites at which these artifacts repeatedly occur are the same sites observed in Neanderthal mtDNA divergence (Pusch and Bachmann 2004). These results indicate that great caution should be exercised in interpreting these early ancient mtDNA sequence data.

Second, these initial ancient DNA studies on human fossils were confined to mtDNA, a molecule that has some unusual patterns of mutation and nucleotide substitution. Most of the analyses of Neanderthal mtDNA have ignored this fact. When the best-fitting maximum-likelihood model of mtDNA evolution is used, there is **no** statistically significant support for a branch separating the Neanderthal sequences from modern human sequences even when all the sequences are assumed to be completely valid (Gutierrez et al. 2002).

Third, mtDNA is incapable biologically of completely reflecting a population's evolutionary history and of rejecting the hypothesis of admixture. MtDNA is sensitive only to female-mediated gene flow and can totally miss even extensive interbreeding mediated through males.

Fourth, as mentioned in the introduction, the evolutionary history of a single gene or DNA region should never be equated to the evolutionary history of a population. A glance at Fig. 3 reveals that much of humanity's recent evolutionary history is not detected at all by mtDNA. One needs multiple loci to obtain an accurate reconstruction of evolutionary history (Wall 2000) and to protect against false inferences due to evolutionary stochasticity and natural selection skewing the results of a particular gene (Templeton 2002, 2004b).

Fifth, the small sample sizes preclude the ability to dismiss significant amounts of gene flow between Neanderthals and moderns (Currat and Excoffier 2004; Nordborg 1998; Pearson 2004; Relethford 2001a; Wall 2000).

Technological advances have overcome many of these problems, as it is now possible to examine much of the nuclear genome with increasing accuracy and coverage (Green et al. 2010; Mendez et al. 2012; Meyer et al. 2012; Reich et al. 2010; Skoglund and Jakobsson 2011; Wall and Slatkin 2012; Yotova et al. 2011). These newer studies on ancient DNA clearly document low levels of admixture with the two archaic populations examined so far: Neanderthals from Europe and Denisovans from Siberia. The fact that two out of two studied archaic populations have contributed to modern human genetic diversity through admixture implies that low levels of admixture between the expanding populations of modern humans with the earlier Eurasian resident populations were both spatially widespread and common. Moreover, ancient DNA studies on an anatomically modern human fossil from China dated to 40,000 years ago revealed admixture levels that were similar to those found in current human populations (Fu et al. 2013). This indicates that admixture was essentially completed before 40,000 years ago. As discussed earlier, modern human fossils are found in China by 110,000 years ago, so the admixture event or processes in China occurred in the time interval between 40,000 and 110,000 years ago. Similarly, a linkage disequilibrium analysis indicates that the last gene flow from Neanderthals into Europeans likely occurred 37,000–86,000 years ago (Sankararaman et al. 2012). These ancient DNA studies confirm the strong rejection of the out-of-Africa replacement model in favor of limited admixture with Eurasian populations made by multi-locus NCPA (Templeton 2002; Templeton 2005).

Demographic Inferences from Coalescent and Simulation Analyses

The definitive rejection by multi-locus NCPA of the null hypothesis of the out-of-Africa replacement hypothesis in favor of a limited amount of admixture (Templeton 2002, 2005) was extremely controversial at the time because the replacement hypothesis had become the standard model of Pleistocene human evolution. The almost universal acceptance of the replacement model by geneticists was all the more remarkable because not a single genetic data set or analysis had resulted in a statistically significant hypothesis test favoring replacement (Templeton 2007). The support for replacement was not based on the standard scientific standard of hypothesis testing, but rather on the weaker argument of hypothesis compatibility with genetic data sets incapable of discriminating among the alternatives (Templeton 2007). The only analysis prior to the ancient DNA studies that claimed a statistically significant rejection of even small amounts of admixture was that of Fagundes et al. (2007) who used computer simulations of several models of human evolution followed by a comparison of how well the specific models fit the genetic data. Such simulation approaches had been frequently used to assess various models of human evolution, but the best-fitting models varied from simulation to simulation, sometimes favoring replacement and sometimes favoring other models (Templeton 2007). The basic problem with these simulations was that there was no rigorous statistical assessment of the goodness of fit, making it impossible to objectively measure how well a particular model fit the data compared to an alternative model. Fagundes et al. (2007) solved this problem by using an approach called approximate Bayesian computation (ABC). The simulation of a model of human evolution requires the specification of a large number of parameters (population sizes, times of range expansions, gene flow rates, degree of admixture, etc.). With ABC, these parameters are regarded as random variables drawn from probability distributions called "priors." After a specific set of parameter values are drawn from the priors, the simulation is executed followed by a comparison of how close a set of summary genetic statistics calculated from the simulation are to the summary statistics calculated from the actual genetic data. This process is repeated multiple times, and from the subset of simulations that result in summary statistics closest to the observed results, it is possible to calculate a localized approximation to the "posterior" distribution of the parameters given the genetic data. Rigorous statistical inference can then be drawn from these posterior distributions. Fagundes et al. (2007) concluded that the replacement model had the highest posterior probability of 0.8 and that any model that included even small amounts of admixture had a posterior probability of only 0.001. These statistically significant results were the opposite of those arising from multi-locus NCPA and are contradictory to the findings of ancient DNA studies.

Egregious statistical errors were made in the analysis by Fagundes et al. (Templeton 2010). The great strength of a Bayesian approach is that prior information can be incorporated into the prior probability distributions. However, Fagundes et al. (2007) did not just ignore prior information, they constructed priors that were contradictory to prior information. For example, as mentioned earlier, already by 2007 there were fossil and archaeological data showing that the expansion of anatomically modern humans out of sub-Saharan Africa had commenced by 125,000–130,000 years ago. Despite this prior information, Fagundes et al. (2007) used a prior that assigned zero probability to any date older than 4,000 generations (80,000 years ago assuming a generation time of 20 years), thereby ensuring a more recent estimated date then indicated by the fossil and archaeological data regardless of the genetic data. Other priors likewise were incompatible with prior studies (Templeton 2010). Much more seriously, Fagundes et al. (2007) used the posterior probabilities in a manner that violated fundamental probability measure theory. In particular, they had a parameter *M* that measured the degree of admixture.

The model with no admixture ($M = 0$) is a special case of the general model in which M can take on any value between 0 and 1. Hence, the $M = 0$ model is nested within the general model. Fagundes et al. (2007) treated the special case and general models as if they were mutually exclusive rather than nested, resulting in posterior model probabilities that were mathematically and logically impossible (Templeton 2010). It is possible to reformulate nested models as mutually exclusive models in a Bayesian framework by performing a Jordon decomposition in which the special case is assigned an atom of probability mass, and the remaining parameter values are assigned a continuous probability measure. No such decomposition was made, so the model probabilities given by Fagundes et al. (2007) have no validity. By using a standard Bayesian procedure that treats nested models as nested models (Lindley 1965), the hypothesis of replacement is rejected in favor of the admixture model with a probability <0.025 (Templeton 2010). This reversal of relative model probabilities by 5 orders of magnitude illustrates the serious nature of the statistical errors committed by Fagundes et al. (2007). Note also that this reversal of inference was made using the *same* posterior distributions generated by Fagundes et al. (2007). Hence, this is not an error of Bayesian statistics in general nor even of ABC in particular. Rather, Fagundes et al. (2007) used their posterior probabilities incorrectly relative to the models being tested. Once this error is corrected, NCPA, ancient DNA, and ABC all result in the rejection of the out-of-Africa replacement model in favor of a model with limited admixture.

ABC and other simulation approaches have the serious disadvantage relative to NCPA that the models of human evolution have to be fully pre-specified rather than having the models emerge naturally from the hypothesis testing framework. However, ABC and other simulation approaches do have the advantages over NCPA that a broader range of genetic data can be used for inference and that they can estimate many important demographic parameters. Because the coalescent process is influenced by basic demographic parameters such as population size and population growth rates, coalescent and simulation analyses have been extensively applied to reconstruct past human demography. These analyses can both reinforce and complement the inferences made from NCPA. For example, NCPA infers a population range expansion out of Africa starting around 130,000 years ago, but it only identifies this as an expansion in geographical range and not necessarily as an expansion in population size. One of the first molecular genetic studies that indicated that this time period was also marked by a population size expansion was the work of Rogers and Harpending (1992). They showed that a sudden increase in population size induces a distinct peak (wave) in the distribution of pairwise nucleotide differences (the mismatch distribution) under a neutral model of evolution in a DNA region, with little to no recombination and with each new mutation occurring at a distinct nucleotide site (the infinite-site model) and uniformly across sites. They found such a distinct peak in human mtDNA, which apparently marks a rapid increase in human population size. Computer simulations of the coalescent under an infinite-site model revealed a good fit to the empirical curve with a population size expansion between 60,000 and 120,000 years ago (later revised to 30,000–130,000 years ago (Harpending and Rogers 2000)), which corresponds well to the most recent out-of-Africa range expansion shown in Fig. 3. They also showed that Tajima's D statistic (Tajima 1989a), an infinite-site model statistic that is sensitive to past population bottlenecks, was consistent with their conclusions of growth from a much smaller population size in the past.

Rogers (1992) recognized that the mismatch analysis and accompanying computer simulations were based upon a highly unrealistic model for mtDNA evolution: the infinite-site model. Rogers (1992) showed that the error introduced by this assumption was only about 3 % and perhaps less than 1 %, a conclusion reinforced by subsequent work (Rogers et al. 1996). In contrast, Yang (1997) and Schneider and Excoffier (1999) found that the estimates of ancestral population sizes are very sensitive to mutational assumptions, with the infinite-site model underestimating past population size. The reason for this discrepancy in how much error is induced is that there are multiple alternatives once one leaves the model of infinite sites and uniform mutation rates. Depending upon the alternative chosen, one can obtain trivial to substantial errors from infinite-site, uniform mutation-based statistics. Unfortunately, our knowledge of the appropriate model for DNA evolution is limited at present; and moreover, different DNA regions normally deviate from the uniform infinite-site model in region-specific ways (Fullerton et al. 2000; Templeton et al. 2000a), so there is no single alternative. We do know now that the deviations from the uniform infinite-site model are much more extreme than those taken into account by Rogers (1992) and Rogers et al. (1996). To illustrate how misleading the infinite-site model can be in a case where the answer is known, Templeton et al. (2000a) applied a standard, infinite-site estimator of recombination to human mtDNA. The infinite-site statistic detected 413 recombination events uniformly distributed over the mtDNA genome. The problem is mtDNA does not recombine! Thus, the conclusions based on infinite-site statistics can be egregiously wrong. Such discrepancies can also be found in human nuclear DNA (Templeton et al. 2000a). Unfortunately, infinite-site statistics still dominate the human (and nonhuman) literature. Until we have a greater knowledge of appropriate DNA models and the development of more statistics and simulation packages that do not assume an infinite-site model (and the willingness of investigators to thoroughly examine their data in order to choose an appropriate mutational model for their specific DNA region, including multi-nucleotide models), demographic conclusions should be regarded as subject to an unknown but potentially substantial degree of error. In contrast, NCPA is based on haplotype trees that use a phylogenetic estimator that does not assume the infinite-site model (Templeton et al. 1992), and as a result such haplotype trees can be used to test hypothesis about the underlying mutational models, including multi-nucleotide models of nonrandom mutagenesis (Templeton et al. 2000b).

The statistics used for demographic inference are also sensitive to natural selection (Harpending and Rogers 2000; Tajima 1989a, b). A dramatic indicator of the potential of selection to bias results can be seen in a coalescent analysis to estimate the amount of population size expansion in recent human evolution based on 612 single-nucleotide polymorphisms (SNPs) (Wooding and Rogers 2002). The SNPs were subdivided into three categories: coding nonsynonymous, coding synonymous, and noncoding DNA regions. The coding nonsynonymous SNPs are generally regarded as the ones most likely to be subject to natural selection. Wooding and Rogers (2002) obtained maximum-likelihood estimates of the ratio of the human population size in the most recent epoch to the population size in an earlier epoch for all three SNP categories. The coding nonsynonymous SNPs yield a ratio of 9900, implying massive population growth. In contrast, the ratios were 0.4 for coding synonymous and 0.6 for noncoding SNPs, implying little or no change in population size. Thus, dramatically different inferences arose among these categories of SNPs that should be differentially sensitive to natural selection. Note also that the inferences least likely to be affected by selection indicated little or no change in population size.

Because selection and demography are confounded in the coalescent-based statistics used for demographic inference, it is important to use cross-validation across multiple loci, just as was done in NCPA. However, cross-validation is probably less effective in protecting against false demographic inferences than in protecting against false phylogeographic inferences using NCPA. At the molecular level, the two most common patterns of selection that are reported in the literature are negative (purifying) and positive (directional) selection (Fay et al. 2001; Miller et al. 2004). Negative selection occurs when mutations at a locus or DNA region are primarily a mixture of neutral and deleterious mutations such that the role of natural selection is to eliminate the deleterious mutations, thereby preserving the important structural features controlled by the gene. About 70 % of all nucleotide substitutions leading to amino acid changes are deleterious in humans and chimpanzees (Enard and Pääbo 2004), and 48 % of the single-nucleotide polymorphisms (SNPs) found in a single genome are deleterious (Subramanian 2012). Because deleterious mutations are eliminated by natural selection, they play little if any role in shaping the haplotype tree (Barton and Etheridge 2004). The NCPA inferences arise from the haplotype tree, and therefore purifying selection does not confound NCPA inferences. The same is not true for population size inferences. The selective elimination of deleterious mutations in a DNA region with little or no recombination (such as mtDNA, and now, much of the human nuclear genome as well (Reich et al. 2002)) mimics the effects of a simple reduction in population size in the past (Charlesworth et al. 1995). Unfortunately, the other most common form of selection, directional or positive selection, also mimics a past reduction in population size (Tajima 1989a). Directional selection causes a selective sweep, eliminating all previous variation within the DNA region that does not recombine with the selected mutation. Since NCPA makes inferences only on the variable part of the haplotype tree with no inferences possible past the coalescent time to a common ancestral molecule, the actual inferences made by NCPA are not affected by selective sweeps except in the rare case of actually sampling a locus in the middle of such a sweep. Thus, while NCPA is expected to be robust to both negative and positive selection, population size inferences are affected by both and *in the same direction*. This shared bias from the two most common forms of reported selection diminishes the effectiveness of cross-validation for demographic inferences. Recall from above that deviations from the infinite-site model also result in underestimates of time and population size (Schneider and Excoffier 1999). Hence, many estimates of past population sizes and their ages are probably underestimates, even when based upon multiple loci.

Two other forms of selection can cause a demographic bias in the opposite direction. The first is balancing selection in which natural selection maintains two or more haplotype lineages or alleles in a polymorphic state. Balancing selection can extend coalescence times into the past, which inflates apparent population size. The coalescent processes within each selected haplotype lineage obey neutral coalescent theory (Hudson 1990), so balancing selection has only a limited impact on the haplotype tree (Barton and Etheridge 2004). Because of the nested clade design used in NCPA, most clades would be unaffected by balancing selection, with only those clades containing different selective lineages (typically only those at the highest level of nesting) being influenced. Hence, NCPA inferences are mostly robust to balancing selection but with some exceptions that should be dealt with via cross-validation. The final type of selection is diversifying selection due to local adaptations in a spatially heterogeneous environment. Such selection also maintains polymorphism in the species as a whole and hence mimics the biases seen with balancing selection. However, unlike balancing selection, this type of selection can create strong geographical correlations and thereby lead to false inferences for NCPA. Multi-locus cross-validation is therefore important in both demographic inference and NCPA to protect against the effects of balancing and spatially diversifying selection.

Cross-validation was used for the mtDNA inference of a population size expansion between 30,000–130,000 years ago. Although some nuclear loci do indeed cross-validate this result (Marth et al. 2003, 2004), others do not (Harpending and Rogers 2000). Recall also that the coalescent analyses of the SNPs least likely to be subject to selection did not indicate a Pleistocene population size expansion (Wooding and Rogers 2002). Similarly, an analysis of 10 noncoding DNA regions (to minimize selection) found no evidence for significant population size expansion in Africa and only nominal significance (without correcting for multiple testing) in Eurasian samples (Pluzhnikov et al. 2002). Harpending and Rogers (2000) attempt to salvage the idea of a Pleistocene population size expansion by arguing that balancing selection is pervasive in the human nuclear genome which, as discussed above, inflates the apparent population sizes of the past and thereby reduces the apparent amount of population growth. This assumption is inconsistent with recent surveys of natural selection that found evidence for positive or balancing selection in only 8 of 132 genes in Eurasians, and 0 out of 132 in Africans (Akey et al. 2004). This explanation is also inconsistent with studies indicating little population size expansion that use noncoding or silent variation that is unlikely to be subject to balancing selection (Pluzhnikov et al. 2002; Wooding and Rogers 2002). More recently, analyses based on whole genome data indicate large effective population sizes going back to at least 250,000 years ago (Li and Durbin 2011). Thus, the evidence for a small ancestral human population size is mixed and a coherent picture has yet to emerge (Pluzhnikov et al. 2002; Wooding and Rogers 2002).

A separate demographic issue concerning the most recent out-of-Africa range expansion shown in Fig. 3 was whether or not it involved a large population coming out of Africa, or a small one. Many genetic surveys show that haplotype diversity is generally much lower in Eurasian populations than in African and that Eurasian populations show more linkage disequilibrium (nonrandom associations between polymorphic sites that can be induced by both small population size and admixture) than African populations. These patterns indicate that the African population coming into Eurasia was relatively small initially (Tishkoff and Verrelli 2003) yet dominated in the subsequent interbreeding with Eurasian populations. These patterns could also mean that the Eurasian population was smaller than the African population during most of the Pleistocene (Relethford 1998), rather than an initial extreme bottleneck. Indeed, studies having a large sample of Africans tend to have much larger estimates of ancestral human population size (Tishkoff and Verrelli 2003), even to the extent to showing no significant or moderate population size growth from the past to the present within Africa (Adams and Hudson 2004; Pluzhnikov et al. 2002). However, an ABC analysis using 20 autosomal regions inferred a strong bottleneck as modern humans expanded out of Africa (Laval et al. 2010). In contrast, an ABC analysis based on 61 loci indicated that there was no major bottleneck in modern humans 130,000 years ago, with at most a 3-fold reduction in population size (Sjodin et al. 2012). Thus, the evidence for a strong bottleneck as modern humans expanded out of Africa is mixed, and a coherent picture has yet to emerge.

A major limitation of many of the coalescent estimators relative to NCPA is that they are based on simulating various demographic models and measuring the fit to the data. Thus, the inference universe is limited to the scenarios that were simulated. Even an excellent fit to the data does not insure that the simulated model is the right one because often several models can fit the data well. For example, Adams and Hudson (2004) pointed out that one of the African populations they studied fit both models of constant population size *and* a variety of growth models, including fivefold growth beginning no earlier than 36,000 years ago. The real weakness of the simulation approach is that it is never possible to simulate all possible scenarios, so many alternative hypotheses are never evaluated at all. For example, few of the simulations performed in the papers referred to in this section take into account the fact that the expanding populations out of Africa interbred with Eurasian populations (recall that the hypothesis of total replacement was rejected with a p-value of less than 10^{-17} and admixture has now been confirmed by ancient DNA studies) nor the long history of gene flow constrained by isolation by distance between African and Eurasian populations that has occurred in the last 650,000 years (Fig. 3). What a simulation includes or excludes can make a large difference. For example, most of these simulations also estimate the time of out-of-Africa expansion around 60,000 years ago – a figure incompatible with the date inferred by NCPA and with the fossil and archaeological record summarized earlier. However, when similar simulation models include the effects of migration and gene flow (as suggested by NCPA, Fig. 3), the estimated date of expansion goes back to 100,000 years ago (Gutenkunst et al. 2009) – a figure now compatible with the confidence interval from NCPA (Table 3). Analyses based on whole genome data also indicate a date between 120,000 and 100,000 years ago (Li and Durbin 2011), further supporting the older date estimated from NCPA.

Based on the literature from the early 1990s (reviewed in Hawks et al. 2000), it is commonplace to find many papers citing a figure of 10,000 for the ancestral human population size and even regarding this population size as a well-established constraint in interpreting human evolution (Pearson 2004). Given that inappropriate DNA models, positive and negative selection, and sampling biases all conspire to underestimate this ancestral human population size, it is now obvious that 10,000 is an underestimate. Indeed, the more recent studies that most thoroughly try to eliminate these biases as mentioned above usually detect no significant to moderate population growth during much of the Pleistocene, particularly in Africa, implying that the human ancestral population size was much greater than 10,000.

The error of regarding the figure of 10,000 as a given constraint on recent human evolution is sometimes amplified by regarding this figure as an estimate of the census size of the human population at that time (Pearson 2004). No coalescent estimator of population size estimates census size; rather, they all estimate the inbreeding effective size. A coalescent event establishes a relationship known in population genetics as identity by descent. Population genetics also makes frequent use of an idealized population characterized by self-compatible hermaphrodites that are randomly mating in an un-subdivided population, all with the same average number and variance of offspring (as described by a Poisson distribution), no selection, discrete generations, and constant population size. These assumptions allow one to derive formulae that describe how a variety of population genetic parameters evolve under genetic drift, including the probability of identity by descent. Of course, real populations, and humans in particular, deviate from this idealized population. Population genetics uses the concept of an effective population size to create a common reference for all real populations. One chooses a particular genetic parameter, such as the probability of identity by descent or the variance in allele frequency from one generation to the next, and observes how this parameter evolves in the real population. Then, one calculates the size of an idealized population that would yield the same parameter values as observed in the real population. The calculated size of the idealized population that mimics the evolution of the parameter of interest in the real population is known as an effective population size (Templeton 2006). It has long been known that deviations from the idealized population can create quantitatively and qualitatively different deviations from census size for different population genetic parameters. For example, an expanding population size tends to decrease the inbreeding effective size (the effective size for the genetic parameter of probability of identity by descent) but increase the variance effective size (the effective size for the genetic parameter of the variance in allele frequency from one generation to the next) (Crow and Kimura 1970). It is incorrect to define "the" effective size as the number of breeding individuals, as done for example by Pearson (2004). Rather, there are many different effective sizes, depending upon the genetic parameter of interest. The effective size estimated from coalescent-based approaches is the inbreeding effective size.

There is no expectation for the inbreeding effective size to equal the census size, nor to equal other effective sizes. The absurdity of equating an inbreeding effective size to a census size is shown by the fact that the inbreeding effective size of Africans alone is larger than the inbreeding effective size of Africans and Eurasians together, as pointed out above. Hence, if we equated these effective sizes to census sizes, we would conclude that more people lived in Africa alone than in Africa plus Eurasia combined! Under realistic circumstances, these effective sizes can differ from one another and from census sizes by orders of magnitude (Braude and Templeton 2009; Templeton and Read 1994). For example, models of demes interconnected by gene flow but with some local extinction and recolonization are applicable to many species, including humans. Such "meta-population" models can greatly reduce inbreeding effective size relative to census size (Wakeley 2004). Indeed, Eller (2002) showed that such a demographic model allows the human census size to be approximately 300,000 through the Pleistocene and still be compatible with an inbreeding effective size of 10,000. Consequently, arguments that a population size of 10,000 is too small to support an African and Eurasian distribution (e.g., Pearson 2004) are without substance even if one accepts an inbreeding effective size of humans of 10,000 – a conclusion itself that is highly questionable. Thus, no coherent picture has emerged from genetic studies concerning the size of Pleistocene hominin populations, but a non-genetic estimate of around half a million individuals (Weiss 1984) is consistent with many of the latest genetic results and the calculations of Eller (2002).

Natural Selection and Adaptive Evolution in Hominin Populations

Adaptive Evolution at the Molecular Level

Coalescence theory and phylogenetics provide a variety of tests to infer the presence and type of natural selection operating at the molecular level, particularly in protein-coding genes (Bamshad and Wooding 2003; Enard and Pääbo 2004; Tishkoff and Verrelli 2003). Indeed, the great abundance of sequence data, not only in humans but in closely related species (outgroup data are frequently required for many of these tests of selection), has allowed massive screening throughout the human genome to identify those genes and DNA regions that were specifically subjected to positive, directional selection in the lineage leading to modern humans and thus were involved in the adaptive transformation of the human species.

Purifying selection that maintains an adaptive genetic state is the most common selective pattern identified, affecting at least 5.5 % of the human genome and millions of elements, including protein-coding exons, RNA structural families, and potential promoter, enhancer, and insulator regions (Lindblad-Toh et al. 2011; Ward and Kellis 2012).

Positive selection, in which natural selection favors a rare preexisting variant as the environment changes or a de novo mutation, is of more interest in understanding the evolutionary changes leading to modern humans. Clark et al. (2003) found 178 genes out of 7,645 protein-coding genes that had significant ($p < 0.01$) evidence of positive selection with standardized ratios of nonsynonymous to synonymous nucleotide substitutions with a model that allowed the amino acid sites to be either neutral, under negative selection, or under positive selection specifically on the branch of the gene tree leading from the common ancestor of humans and chimpanzees to present-day humans. Many of the genes that were under positive selection in the human lineage involved sensory perception, particularly olfaction and hearing. Several other genes under positive selection were involved in amino acid catabolism and may have been selected as the dietary habits of the human lineage diverged from the human/chimp ancestral state. Many developmental genes were also under positive selection in the human lineage, and these fell into two main categories: skeletal development and neurogenesis. Using a more extensive genomic database, Grossman et al. (2013) identified 412 candidate regions for positive selection, including 35 high-scoring nonsynonymous variants, 59 variants associated with expression levels of a nearby coding gene or lincRNA, and numerous variants associated with susceptibility to infectious disease and other phenotypes. Looking specifically at genes involved in the nervous system, Dorus et al. (2004) found accelerated rates of amino acid substitutions in the primate lineages leading to humans, with the highest rate being found in the branch leading from the common ancestor of humans and chimpanzees to humans. Vallender and Lahn (2004) reviewed the literature on those genes showing positive selection in the lineages leading to humans and found that the vast majority of them fell into just a few functional categories: host-pathogen interactions, reproduction, dietary enzymes, sensory perception, central nervous system functioning, and brain anatomy.

The above studies indicate that positive selection played an important role in the adaptive evolution of the human lineage, but these studies only localize that selection into the time period between the common ancestor of humans and chimpanzees to the present. One way of localizing the positive selection to the Pleistocene is to look for evidence of a selective sweep and genomic segments of identity by descent that are shared by diverse individuals and populations. As mentioned in the previous section, positive selection induces a selective sweep of the genetic variation linked to the favored mutation. This in turn leaves a signature in the haplotype tree that is gradually lost over time, limiting this approach to only the latest stages of human evolution (Przeworski 2002). Such selective sweeps have been found for the *monoamine oxidase A* gene (Gilad et al. 2002), involved in the functioning of the central nervous system, and in *FOXP2*, a gene coding for a transcription factor involved in speech and language development (Zhang et al. 2002). Another region of accelerated evolution in the human lineage is a novel RNA gene that is expressed in the developing human neocortex from 7 to 19 gestational weeks, a crucial period for cortical neuron specification and migration (Pollard et al. 2006). The HLA region shows the most extreme signal, suggesting that much of the strong recent selection acting on the human genome has been immune related (Albrechtsen et al. 2010).

A second approach to identifying recent selection is to look for evidence of positive selection confined to Eurasian populations. This would not only imply some sort of local selection involved with the colonization of Eurasia but also confine the time period to the last 2 Myr. Akey et al. (2004) surveyed 132 genes and found evidence for positive or balancing selection in eight of them in Eurasian populations, but none in African populations. Similarly, a survey of 624 autosomal loci found evidence of positive selection in 13 genes, and of these 12 exhibited only a Eurasian signature of positive selection (Storz et al. 2004). A contrast of East Asian populations identified positive selection resulting in a north-south cline in the HLA region (Suo et al. 2012). A genome scan of human populations of African, European, and Asian origin found evidence of selection related to population-specific traits, such as skin pigmentation, immune response, senses, and dietary adaptations (de Magalhães and Matsuda 2012), and another study indicated selection related to cold tolerance (Hancock et al. 2011). Specific to dietary adaptations, the enamelin gene that influences enamel formation has been shown to undergo bursts of positive selection in primates inferred to have undergone dietary change, and similarly it shows evidence for selective sweeps in non-African populations (Kelley and Swanson 2008). With respect to immune response, 11 out of 26 blood group antigen genes show significant correlations with local pathogen richness, and 3 show evidence of balancing selection in which selection favors the maintenance of multiple allelic lineages, a type of selection also found in HLA (Fumagalli et al. 2009) and the TRIM5 gene that encodes a retroviral restriction factor that influences risk of certain viral infections (Cagliani et al. 2010). A subsequent genome screen demonstrated that selection on pathogens is the primary driver of local adaptation and affects the distribution of genetic variation at a large number of genes (Fumagalli et al. 2011). These studies indicate that human populations had to adapt to novel selective features associated with the Eurasian continent. Thus, the expansions out of Africa shown in Fig. 3 were also associated with altered selective regimes that influenced human adaptive evolution.

A third approach to identifying genes under positive selection is to make use of the genome data available from ancient DNA studies. Paixao-Cortes et al. (2012) performed an extensive comparison of the complete genomes of chimpanzee (*Pan troglodytes*), extant *Homo sapiens*, Neanderthals, and the Denisova specimen. They focused on nonsynonymous mutations in protein-coding genes and found 10,447 nonsynonymous substitutions in which the derived allele is fixed or nearly fixed in humans as compared to chimpanzee. By restricting their study to derived alleles that were fixed or near fixed in humans, this study focuses only on those genes that were selected in the entire human lineage and that were not involved in local adaptation. The presence of the derived alleles was then searched for in the two archaic genomes, and in most cases it was found. This indicates that the selective sweeps that gave rise to modern humans were initiated before the divergence of archaic and modern humans and/or there was sufficient gene flow between archaic Eurasian and African populations that selectively favored alleles could spread between them.

Adaptive Evolution of Hominin Facial Morphology

When selection operates upon a morphological trait, it generally alters other traits as well, due to shared underlying developmental process and genes. These correlated responses to selection can be captured by a quantitative genetic variance/covariance matrix (Ackermann and Cheverud 2004). If a set of morphological traits is evolving neutrally or are neutral correlates of another, unmeasured trait under selection, then their coordinated change should reflect the variance/covariance matrix (Lande 1980). Deviations from this expected correlational structure indicate the action of natural selection. Ackermann and Cheverud (2004) estimated the variance/covariance matrices for several facial features from living human, chimpanzee, and gorilla populations and used all three of these living models to detect selection on facial features in hominin fossils. The results within the *Homo* fossils were robust to all three models, showing that between 1 and 2 Ma, most facial evolution was neutral. In contrast, selection was necessary to produce the *Homo* face from that of a gracile australopith, with selection being exerted to increase the relative portions in the upper face and orbit, weak to no selection to increase the midface/nasal region, and selection to reduce the lower orbits and zygomatics. Hence, in terms of the human face, the most important adaptive evolution occurred leading up to *Homo*, with little evidence for selection during the Pleistocene. This is consistent with the idea that the development of cultural inheritance could have released many morphological traits of humans from the effects of selection (Ackermann and Cheverud 2004; Lynch 1990). If this explanation is true, it would imply that hominins increasingly relied on technology near the time of the spread of *Homo erectus* out of Africa.

Conclusions

The first major event in hominin evolution over the past 2 Myr was a range expansion out of the African homeland into Eurasia. This expansion event may have been triggered by an increase in the importance of cultural inheritance as a means of adapting to the environment. Regardless, the time of this expansion marked an era of relaxed selection on some morphological features. Although some morphological selection may have been relaxed as hominins expanded into Eurasia, natural selection nevertheless operated strongly and swiftly upon many genes as hominins adapted to novel environmental circumstances in Eurasia and underwent multiple global selective sweeps.

Because this initial colonization of Eurasia left detectable genetic signatures in present-day Eurasian populations, there has been a continuous Eurasian hominin presence for at least the last 1.9 Myr. Africa still remained the center of hominin evolution, however, with the next major Pleistocene event being the development of the Acheulean culture and its subsequent spread out of Africa. This spread was both cultural and demic, with the expanding peoples from Africa interbreeding with at least some of the Eurasian populations with whom they came into contact.

Recurrent gene flow with isolation by distance was established between African and Eurasian populations after the Acheulean expansion 650,000 years ago. Such a population structure would have allowed some traits to spread throughout all of humanity, while other traits were locally restricted. Indeed, those derived alleles that went to fixation or near fixation in modern humans are for the most part shared with archaic Eurasian populations. For other genes, there is evidence of local selective sweeps, often confined to Eurasia despite recurrent gene flow. No coherent picture has emerged from genetic studies concerning the size of the middle Pleistocene hominin population, but a non-genetic estimate of half a million individuals (Weiss 1984) is consistent with many of the latest genetic results.

Many anatomically modern traits first evolved in Africa, and then populations with these traits spread out of Africa starting 130,000 years ago. As with the Acheulean expansion, this expansion involved interbreeding with at least some archaic Eurasian populations and was overlaid upon a recurrent pattern of genetic interchange. Modern traits could spread by this demic expansion coupled with admixture and gene flow with isolation by distance. As before, this population structure allows locally adaptive traits to maintain their regional continuity.

After this last major out-of-Africa expansion event, humans expanded into previously unoccupied parts of the world: northern Eurasia, Australia and the Pacific, and the Americas (Fig. 3). There was also a major expansion of humans out of Asia back toward Europe and Africa that was primarily male-mediated (Fig. 3). Wherever humans spread, genetic interconnections were maintained with other human populations, at least on a time scale of several thousands of years. These connections of gene flow were restricted through isolation by distance, although long-distance dispersal becomes more important in very recent times (Table 2). Even today geographical distance remains the primary indicator of the degree of genetic differentiation between local human populations (Eller 1999). The relationships among current human populations therefore cannot be represented as a tree of populations, but rather an intertwined trellis (Fig. 3). As a result, humanity evolved into its modern form as a single evolutionary lineage but with some geographical differentiation at any given time.

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Cross-References

- ▶ Ancient DNA
- ▶ Genetics and Paleoanthropology
- ▶ Origin of Modern Humans
- ▶ Overview of Paleolithic Archaeology
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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Dispersals of Early Humans: Adaptations, Frontiers, and New Territories

Michael Bolus

Contents

Abstract

Fossils of early hominins have been found exclusively in Africa. While the australopiths only spread within Africa, members of the genus *Homo* were the first to leave their home continent, roughly 2 million years ago, thus expanding their settlement area considerably. Once "out of Africa," groups of *Homo ergaster*, *Homo erectus*, or other early *Homo* species moved in several waves to East and Southeast Asia, while other groups, possibly through the Levantine Corridor and crossing the Caucasus, entered Europe. The oldest artifact assemblages outside of Africa are of Oldowan type, while in Africa at the same time the techno-complex of the Acheulean had begun to evolve, which came to

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M. Bolus (✉)
Heidelberg Academy of Sciences and Humanities, Research Project ROCEEH at the University of Tübingen, Tübingen, Germany
e-mail: michael.bolus@uni-tuebingen.de

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Eurasia much later. In Europe, the Neanderthals, the only indigenous European hominins, evolved out of later populations of *Homo heidelbergensis*. At the end of the last glacial period, the Neanderthals enlarged their originally exclusive European settlement area, expanding into the Near East, parts of Central Asia, and even as far as the Altai region in Siberia. While the Neanderthals apparently never entered Africa, they started their movement "out of Europe" and into Asia at about the same time that anatomically modern humans (AMH), who originated in Africa, started their movement "out of Africa," also heading first into Asia. Sahul was colonized by AMH earlier than Europe, which was first entered about 45,000 years ago, when the Neanderthals were still living there. Today, modern humans are the only existing hominin species, inhabiting nearly every part of the world. During their expansions, the Neanderthals and AMH not only mixed with each other – at least in the Near East – but apparently both interbred with a third hominin group, the Denisovans, who seem to have moved specifically into East and/or Southeast Asia.

Introduction

Broad agreement exists on the fact that the human lineage originates from Africa. All hominin species which are potentially direct ancestors of the genus *Homo* have been found exclusively on this continent. Similarly, the first known stone tools, with an age of about 2.6 million years, have been found in East Africa. It seems plausible that this cultural "quantum leap," which represents a very specific type of adaptation, enabled early humans – most probably the earliest representatives of the genus *Homo* (for an overview of the genus *Homo* see, e.g., Wood and Baker (2011) and Henke and Hardt (2012)) – to become increasingly independent from climates and environments and to colonize new territories. The question of when, why, and how early hominins started to leave their original home ranges has been and still is a topic of vivid discussion within paleoanthropology, archaeology, and related scientific fields. While the australopiths only spread within Africa (Schrenk et al. 1993, 2002; Vrba 1995), early *Homo* left his home continent to settle large parts of the Old World in several waves (see Tattersall 1997). The Neanderthals, originating from Europe, widened their settlement area considerably while it was left to anatomically modern humans (AMH), rooted in Africa once more, to colonize nearly all parts of both the Old World and the New World.

Prelude: African Origins

As far as is known, the earliest ancestors of humans evolved in tropical Africa. A group of Late Miocene fossils, *Sahelanthropus tchadensis* (Chad), *Orrorin tugenensis* (Kenya), *Ardipithecus kadabba*, and *Ardipithecus ramidus* (both Ethiopia), with ages between about 7 and 4.4 million years, is probably ancestral to the Australopithecines (Brunet 2009) and was able to walk at least occasionally upright (see Harcourt-Smith, chapter "▶ Origin of Bipedal Locomotion," Vol. 3).

Starting with *Australopithecus anamensis* from East Africa about 4 million years ago, the genus *Australopithecus* developed as the earliest known undoubted hominins. Today, several species of these gracile hominins are known, among them *Australopithecus afarensis* and *Australopithecus africanus*. The famous 3.5-million-year-old partial skeleton known as "Lucy" belongs to the former group, whereas the somewhat younger Taung Child is a representative of the latter (for an overview, see Klein (2009); Kimbel, chapter "▶ The Species and Diversity of Australopiths," Vol. 3). Another genus, *Paranthropus*, evolved shortly after 3 million years ago in East Africa, with members of the genus *Australopithecus* as their ancestors. Later representatives of *Paranthropus* existed in East and South Africa 1.4 million years ago. Isotopic analyses have shown that *Australopithecus* and *Paranthropus* consumed different types of diet (Sponheimer et al. 2013), which most probably reflects different modes of living and different patterns of adaptation.

From an anthropological point of view, it is difficult to distinguish clearly between late australopiths and early representatives of the genus *Homo*. The challenge has been highlighted by the recent discovery of two approximately 2-million-year-old skeletons in the South African cave site of Malapa named *Australopithecus sediba* (Berger et al. 2010), which combine features of australopiths with those of early *Homo*.

It can be shown that australopiths and *Paranthropus* already left their home areas to colonize new territories (see, e.g., Schrenk et al. 2002), but they stayed within their continent. Until now, there is no unambiguous indication that representatives of the genus *Australopithecus* (and of the genus *Paranthropus*) ever moved out of Africa. The possibility cannot, however, be completely ruled out.

Out of Africa: Early *Homo*

The oldest known *Homo* fossil so far was discovered in the "Hominid Corridor" in northern Malawi. It is the mandible UR 501 from Uraha, attributed to *Homo rudolfensis* and dated to an age of about 2.5 million years (Schrenk et al. 1993). Together with the discovery of *Paranthropus*, probably *P. boisei*, of more or less the same age in Malema, also in northern Malawi, this has high biogeographic significance, and it has been suggested (Bromage et al. 1995, p. 71) that "early hominids arose successively in the eastern African tropical ecological domain. During favorable periods, some early hominids dispersed southward beyond the Zambesian Ecozone, evolved there, perhaps due to relative isolation and/or due to factors associated with its temperate ecology, and became endemic there."

The earliest *Homo* appeared at about the same time as the oldest stone tools. They come from Gona in Ethiopia and have an age of about 2.6 million years (Semaw et al. 2003). The assemblage consists of cores, flakes, and pebble tools which can be attributed to the early Oldowan complex (named after the Olduvai Gorge in Tanzania). Some bones of the associated fauna show unambiguous cut marks made by humans processing the bones. Only slightly younger are early Oldowan assemblages from Lokalalei 2C in West Turkana (Kenya) with an age of about 2.34 million years. The choice of raw materials and the level of knapping skills these early humans mastered demonstrate a high degree of planning and foresight at that early date (Delagnes and Roche 2005). It is still not definitely clear which hominin species was responsible for the earliest stone tools. A first lower molar germ attributed to early *Homo* found near Lokalalei 2C makes early members of our genus possible candidates for making the artifacts, but *Paranthropus/ Australopithecus aethiopicus* was also present in West Turkana about 2.5 million years ago. As far as the Gona artifacts are concerned, *Australopithecus garhi*, known from Bouri (Ethiopia), may be another possible candidate. While no stone artifacts have been found in direct association with *H. rudolfensis* fossils, *H. habilis* has securely been identified as toolmaker.

In any case, stone tools and cut marks on large mammal bones suggest that early *Homo* had a dietary spectrum different from that of other early hominins. Isotopic analyses (Balter et al. 2012) have confirmed that *Paranthropus robustus* relied more on a plant-based diet than early *Homo*, which in turn means that early *Homo* consumed more meat than contemporary *Paranthropus*, thus occupying a different ecological niche. Tool use may also have been crucial in enabling early *Homo* to colonize new territories – ones never settled before by hominins. Another factor could be the use of fire. Although the oldest secure evidence for the controlled use of fire dates no earlier than about 1 million years ago (Wonderwerk Cave in South Africa: Berna et al. 2012), it is imaginable that early *Homo* already had at least the ability to use fire started by natural processes such as lightning. This might have helped him, a carnivore himself, to keep other large carnivores away, thus gaining access to carcasses of mammals hunted by others and, ultimately, to win and defend territories occupied by other large carnivores.

About 2 million years ago, or perhaps a bit earlier, early *Homo* left the African continent for the first time. The exact timing and circumstances of that first wave(s) out of Africa are still unclear. It may be that they were pushed out by climatic conditions. Helmut Hemmer regards coevolution with felids and canines (predators) as the essential trigger. According to him, early *Homo* as a member of the guild of larger terrestrial carnivores, and as such dependent on animal food resources, followed large herds, in competition with other larger terrestrial carnivores and finally left Africa (Hemmer 2000). The role that fire use may have played in this process has just been mentioned. Another question that is still unsolved is which species of *Homo* took the first step. It is even possible that different species found their way out of Africa.

Roughly contemporaneously with this first wave of dispersal, a new lithic technology developed in Africa. First and foremost, it is characterized by bifacially worked hand axes. After the site of St. Acheul in northern France, this new techno-complex is named Acheulean. While until recently it was thought that this technology started at about 1.6 million years ago, excavations at the site of Kokiselei 4 in Kenya have yielded evidence for an earlier origin at about 1.8 million years ago (Lepre et al. 2011).

The oldest human fossils outside Africa are those from Dmanisi in the Caucasus in Georgia, associated with faunal remains and stone artifacts and about 1.8–1.7 million years old (Ferring et al. 2011). There has been some debate about the exact taxonomic position of these fossils (see Tattersall, chapter "▶ *Homo ergaster* and Its Contemporaries," Vol. 3); both similarities and differences with *H. ergaster* and *H. erectus* have been suggested. In earlier publications (e.g., Gabounia et al. 2002), the fossils were ascribed to a new *Homo* species: *H. georgicus*; however, in the context of the detailed analysis of skull 5, the denomination *H. erectus ergaster georgicus* was suggested (Lordkipanidze et al. 2013). The lithic industry is dominated by pebble tools, cores, and flakes, whereas retouched pieces are rare; it thus represents a typical Oldowan. This clearly proves that intercontinental dispersals were possible with such a relatively simple tool kit and that no (Acheulean) hand axes were needed. Since the earliest Oldowan tools are almost 1 million years older than the Dmanisi tools, this also suggests that lithic technology alone was not sufficient for *Homo* to leave Africa; the earliest toolmakers must have faced other obstacles that hindered them from crossing the continental frontier. Given the fact that hand axes already existed 1.8 million years ago in Africa, the first wave of dispersal is obviously not linked with hand axe-producing humans. According to a hypothesis proposed by Helmut Hemmer (e.g., Hemmer 2000), this could mean that the earliest *Homo* populations out of Africa relied completely on scavenging to cover their meat requirements and that they were in constant competition with larger predators, since the Oldowan tool kit does not include the unambiguous weapons that seem necessary to enable hominins "to enjoy nearly unlimited large mammal food resources" (Hemmer 2000, p. 99).

The implications of an early origin of the Acheulean are discussed in some detail by Lepre et al. (2011, pp. 84–85). They argue that "the difference between the ages for the oldest known Acheulian artefacts in the world from Africa and the oldest known Acheulian artefacts from Eurasia raises the likelihood that the first Eurasian hominins derived from an African population lacking Acheulian culture. Potentially, two hominin groups coexisted in Africa at 1.76 Myr ago. One of these groups could have developed the Acheulian technology but remained in Africa. The other could have lacked the cognitive ability and/or technological knowledge to manufacture the Acheulian technology and did not carry it into Eurasia. This division may indicate different behavioral aptitudes for separate African species (for example, *H. erectus sensu lato* versus *Homo habilis sensu lato*) or a within-species cultural disparity. In any event, it seems that a second hominin dispersal with Acheulian technology or a diffusion of this technology took place later, leading to the widespread occurrence of this Early Stone Age tradition in the circum-Mediterranean area and elsewhere after ~1 Myr ago."

Some sites in China and Java are only a bit younger than Dmanisi and may also be part of the first wave(s) of dispersal. They include several 1.6- to 1.5-million-year-old sites in the Nihewan Basin in northern China with faunal remains and Oldowan-type stone artifacts (Keates 2010; Ao et al. 2013), as well as the oldest *H. erectus* fossils from the Sangiran Dome, found without archaeological context and also with ages of ca. 1.6–1.5 million years (Larick et al. 2001).

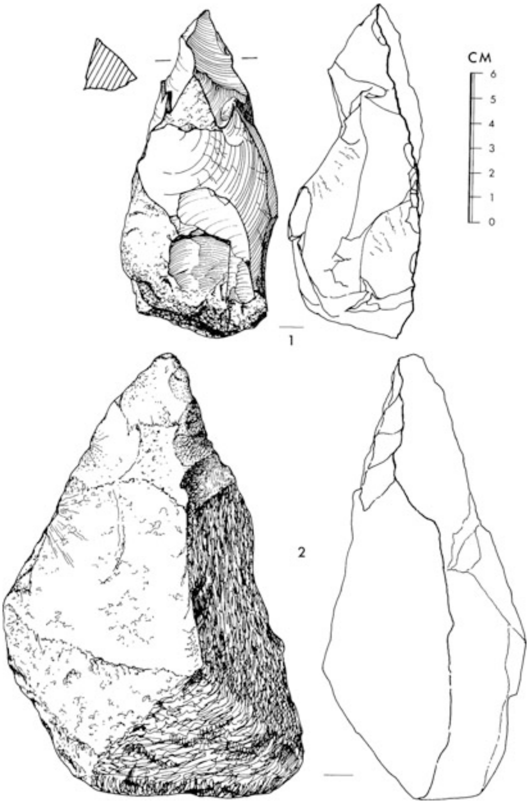


Fig. 1 ‘Ubeidiya. Acheulean hand axes from layer I-26d (After Bar-Yosef and Goren-Inbar 1993. Reproduced with kind permission from O. Bar-Yosef and N. Goren-Inbar)

A late witness of the first wave(s) of expansion of early *Homo*, or maybe an early witness of the next wave, is the site of ‘Ubeidiya in the Jordan Valley in Israel, which is situated along one of the possible dispersal routes out of Africa, the so-called Levantine corridor. Paleomagnetic studies at the multilayered site indicate a sequence spanning between around 1.5 and 1.2 million years. Early *Homo* remains associated with rich lithic artifact assemblages, and faunal remains have been uncovered (see, e.g., Belmaker et al. 2002). The lithic assemblages combine elements of the Developed Oldowan with hand axes as markers of the early Acheulean (Bar-Yosef and Goren-Inbar 1993) (Fig. 1). Recently, evidence has been published that already during the same period, the Acheulean may have reached the Indian subcontinent (Pappu et al. 2011). Assuming that the early date will be confirmed, this Acheulean presence in South Asia may be due to a rapid dispersal of early humans from ‘Ubeidiya, but there is also the possibility of another direct dispersal wave from Africa (see Dennell 2011).

It is interesting to note that the first human settlement of Europe is obviously not linked with the first dispersal wave out of Africa, but that nevertheless no Acheulean assemblages akin to those already present in the Near East have been found in the earliest European sites. If the dates of down to 1.4–1.3 million years for the

Spanish sites of Barranco León D and Fuente Nueva 3 in the Orce region are correct, these range among the sites providing the earliest evidence for human presence in Europe. The lithic assemblages from these sites do not show any Acheulean influence but clearly are of Oldowan type (Barsky et al. 2010). With an age of older than 1.2 million years – probably close to 1.4 million years – an early *Homo* molar found at Barranco León D seems to be the oldest human fossil in Europe today (Toro-Moyano et al. 2013). Of apparently similar age are the Oldowan assemblages from Pirro Nord in southern Italy (e.g., Arzarello et al. 2012).

As far as Europe is concerned, Oldowan-type assemblages remain the only assemblages to be found with the sites following chronologically, the long existence of the Oldowan being a demonstration of the effectiveness of this technology. This is, for instance, true for the 1.2-million-year-old Sima del Elefante site in Atapuerca and still true for the 0.8-million-year-old Gran Dolina site in the same Atapuerca complex. Both sites have yielded human fossils, with those from the latter site often attributed to a separate species: *Homo antecessor* (see, e.g., Bermúdez de Castro et al. 1997).

The sites mentioned above are clear indications of a relatively early settlement of Europe, at least as far as the southern part of the continent is concerned – a settlement taking place at a much earlier time than the supporters of a "short chronology" for the settlement of Europe had suggested (for an overview, see Roebroeks 2006).

One of the next dispersal waves may be represented by the site of Gesher Benot Ya'aqov in Israel. About 780,000 years old, the assemblages of this site are clearly Acheulean (Sharon et al. 2011). Having yielded the oldest secure evidence for the controlled use of fire outside Africa, this site indicates that at least some 800,000 years ago, continual fire control was part of the capabilities of early hominins in Eurasia. Given the fact that the earliest evidence in Africa seems to be older than 1 million years, it seems plausible that both the Acheulean technology and the controlled use of fire mark important developments needed for early humans to conquer new territories during further dispersals. Acheulean-like hand axes found in the Bose Basin in China (Yamei et al. 2000) are of about the same age as the assemblages from Gesher Benot Ya'aqov. With a possible early appearance of the Acheulean in India, as mentioned above, these tools might not be the result of an indigenous development but may well be due to the "movement of hominins (or ideas) from either East Africa or the Levant. This raises the possibility that the Acheulian-like bifaces from China indicate subsequent dispersal from India" (Dennell 2011, p. 1532).

An early appearance of Acheulean hand axes has been claimed for the Spanish sites of Cueva Negra del Estrecho del Río Quípar and Solana del Zamborino (Scott and Gibert 2009). However, the early dates of 0.9 million years for the Quípar site and 0.78 million years for the Zamborino site have been plausibly questioned by other scientists (Jiménez-Arenas et al. 2011) and thus cannot be taken as proof for such an early presence of the Acheulean in Europe. Acheulean hand axes from fluvial deposits in the Middle Loire River Basin in France may date back to

700–600,000 years ago (Despriée et al. 2011), but with the possible exception of the 650,000-year-old Notarchirico site in southern Italy (Lefèvre et al. 2010) and of a single hand axe from Sima de los Huesos at Atapuerca, the earliest securely dated in situ Acheulean levels from Europe are not considerably older than 500,000 years (Antoine et al. 2010; Falguères et al. 2010). Again, it is noteworthy that between about 800,000 and 600,000 years ago, dispersal waves into the Near East (and to East Asia?) seem to be associated with Acheulean technology, whereas it is questionable if these waves ever reached Europe.

While the earliest secure evidence for the Acheulean in Great Britain is about 500,000 years old (McNabb 2013), the stone artifacts from the Happisburgh 3 site seem to be of Oldowan type rather than representing the Acheulean (Parfitt et al. 2010). In any case, sites such as Happisburgh 3 strengthen the evidence that early humans peopled large parts of Europe rather quickly and even reached regions as far north as Britain nearly 800,000 years ago – again arguing against a short chronology. This remarkable expansion of their settlement area proves that the potential of early hominins to thrive in different landscapes and environments had enormously increased.

Claims have been made in several publications that the Acheulean presence outside of Africa could be seen as an indication of hominin dispersals from Africa into Eurasia. This assumption was strengthened by model-bound approaches and a phylogeographic analysis (Lycett and von Cramon-Taubadel 2008; Lycett 2009). Other studies, however, point to the possibility of local invention and evolution of bifacials in the European Acheulean (e.g., Nicoud 2013).

From the anthropological point of view, the European fossils associated with the Middle Pleistocene Acheulean belong to *H. heidelbergensis*. While the famous mandible from Mauer with an age of about 600,000 years was found without any archaeological context, the fossils from Sima de los Huesos/Atapuerca, Boxgrove, and other sites are secure evidence of this association. The European fossils of *H. heidelbergensis* may be representatives of one of the last (if not the last) expansion wave(s) of archaic humans out of Africa.

Out of Europe: The Neanderthals

Based on the present fossil evidence, the Neanderthals were indigenous European hominins (the only ones) whose origins can be seen exclusively on this continent. They probably evolved from late populations of *H. heidelbergensis* or archaic *Homo sapiens* (see, e.g., Hublin 1998; Rightmire 1998; Bräuer 2008; Harvati, chapter "▶ Neanderthals and Their Contemporaries," Vol. 3). Following the high age estimate for the human remains from Sima de los Huesos in Atapuerca (Spain) (Bischoff et al. 2007), first fossils with diagnostic Neanderthal traits – and thus, the Neanderthal lineage – may be tracked as far back as around 500–600,000 years. During a process that might be called "neanderthalization" and which is described within the "accretion model" (see, e.g., Dean et al. 1998 and Hublin 1998), more and more Neanderthal traits accumulated until during the last glacial the Classic Neanderthals appeared. Based on the accretion model, three categories have been established (see also Serangeli and Bolus 2008):

1. *Pre-Neanderthals* are fossils of *H. heidelbergensis* or archaic *H. sapiens* which show first distinct Neanderthal features. While they are not Neanderthals themselves, they stand at the threshold of what might be referred to as Neanderthals. Besides Sima de los Huesos, sites with pre-Neanderthal remains include Arago (Tautavel) in France, Petralona in Greece, and Steinheim in Germany.
2. *Early Neanderthals* appear around 250,000 years before present (BP) and can clearly be distinguished from *H. heidelbergensis*/archaic *H. sapiens*. The term Early Neanderthals is used for all pre-Weichselian/pre-Würmian Neanderthal fossils. Among the earliest are the fossils from Grotte du Lazaret near Nice (France) and from Pontnewydd in Wales. Similarly, all fossils from the Eemian interglacial, such as the human remains from Krapina in Croatia, are regarded as Early Neanderthals.
3. *Classic Neanderthals* appear starting with the last glacial, some 115,000 years ago. Among the best known and studied is the type specimen discovered in the German Neander Valley (Neandertal) in 1856. Fossils of Classic Neanderthals are spread over larger parts of Europe and can also be found in the Near East, in the western part of Central Asia, and even in the Siberian Altai region.

For the purpose of this chapter, it is sufficient to equate the time of the Neanderthals with the Middle Paleolithic, although this is problematic for some regions. In the Near East, for instance, both Neanderthals and early AMH produced artifact assemblages classified as Middle Paleolithic. But on the other hand, no unambiguous Neanderthal fossils have been found in fully Upper Paleolithic assemblages yet. According to the approach suggested by Alain Tuffreau (1979), Gerhard Bosinski (1986), and others, the Middle Paleolithic started about 300,000 years ago and lasted until about 30,000 BP, at which point its end overlaps with the beginning of the Upper Paleolithic.

Stone tools produced by Neanderthals show a broad variety and include hand axes and other bifacial tools, such as wedge-shaped knives (*Keilmesser*) and leaf points (*Blattspitzen*), different types of side scrapers, variable point types, and many others (Bordes 1961; Bosinski 1967; Fig. 2). Formal organic tools are much rarer. In most cases they are represented by points. While pigment use by Neanderthals is observed relatively often and can be traced backed to Early Neanderthals, personal ornaments are restricted to a small number of late Neanderthal sites. Neanderthal burials which appear just a bit later than the oldest AMH burials give insight into the spiritual world of the Neanderthals.

A map showing all sites with Neanderthal fossils known from the literature highlights the core area of Neanderthals in southern and southwestern Europe (Fig. 3). As indicated by this core area, Neanderthals originally were adapted to a temperate rather than cold, or even extremely cold, climate. However, under

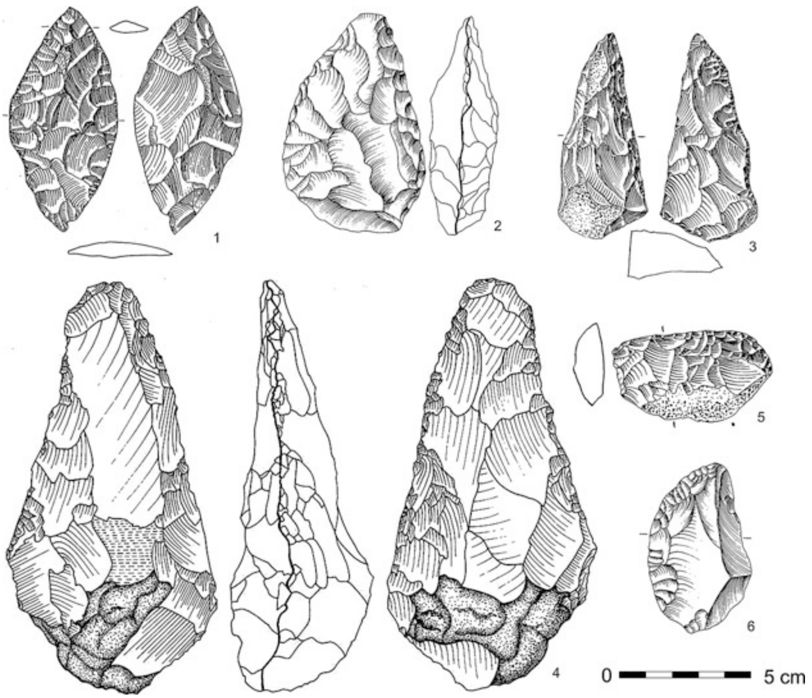
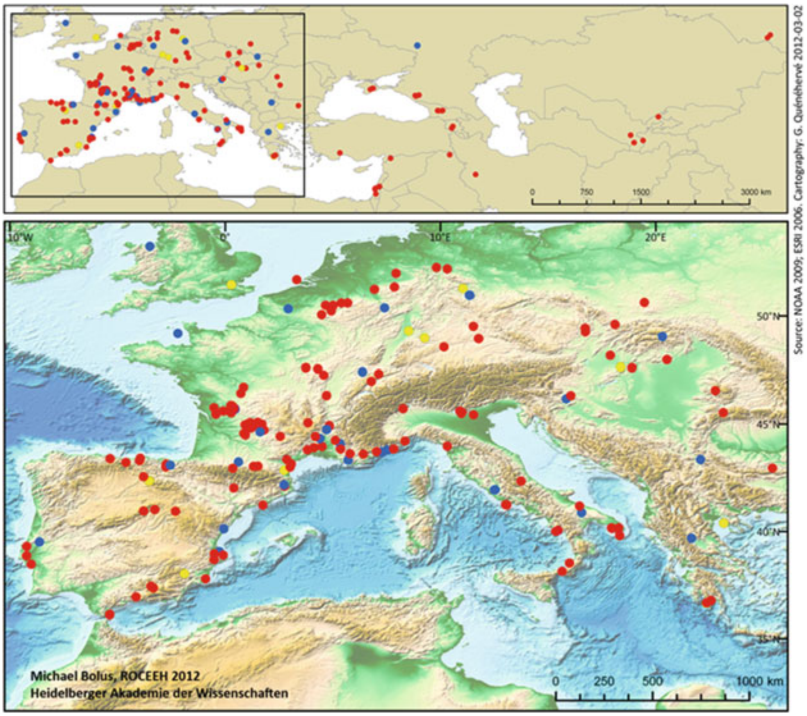


Fig. 2 Middle Paleolithic tools made by Neanderthals from sites in the Swabian Jura, southwestern Germany. *1* Leaf point (*Blattspitze*); *2*, *4* hand axes; *3* wedge-shaped knife (*Keilmesser*); *5*, *6* side scrapers (After Conard et al. 2012)

favorable climatic and environmental conditions, they repeatedly left their core area to move into areas of temporary occurrence *sensu* von Koenigswald (2003) and even "learned" to cope with harsher environmental and climatic conditions. During the last glacial, Classic Neanderthals enlarged their originally exclusive European settlement area, expanding into the Near East, parts of Central Asia, and even as far as the Altai Mountains in Siberia – a dispersal that has been called the "Out of Europe Movement" of Neanderthals (Serangeli and Bolus 2008).

It is remarkable that, on the one hand, Neanderthals were able to settle new territories, but that, on the other hand, there is no unambiguous evidence that they ever moved to Africa, the home continent of AMH (although some anthropologists think there are Neanderthal influences, however slight, in North Africa: Simmons and Smith 1991). The reasons why Neanderthals did not enter Africa once they had reached the Near East about 80–90,000 years ago are not yet clear; they represent one important topic of the research project "The role of culture in early expansions of humans" (ROCEEH) of the Heidelberg Academy of Sciences and Humanities



Source: NOAA 2009; ESRI 2006. Cartography: G. Quénéhervé 2012-03-02

Fig. 3 Distribution of pre-Neanderthal (*yellow dots*), Early Neanderthal (*blue dots*), and Classic Neanderthal (*red dots*) fossils

(Haidle et al. 2010). It is obvious that AMH lived in northern Africa when Neanderthals settled Europe and moved "out of Europe." Hence, it might be possible that some sort of "cultural barrier" plays an important role in the lack of Neanderthals in northern Africa and in Africa in general.

As remarkable as the extensive expansion(s) of Neanderthals is their disappearance as an independent hominin lineage some 30–35,000 years ago or, according to other scientists, some 40,000 years ago (see Pinhasi et al. 2011). It is even more striking given the fact that at the same time when Neanderthals reached their largest geographic distribution in the Siberian Altai Mountains (Fig. 4), their demise had already started in their home continent, Europe. Their distribution area contracted further and further, until finally Neanderthals only existed in some refuge areas such as the Iberian Peninsula and the Crimea.

There have been vivid discussions and speculations about the reasons for the extinction of the Neanderthals, but it must be admitted that these reasons are not yet fully understood. It is most probable that the answer lies in an interaction of several factors. One of these factors might be the appearance and rapid expansion of AMH in Europe starting some 45,000 years ago.

Fig. 4 Okladnikov Cave in the Russian Altai Mountains. Together with two other caves from the same region, the site marks the easternmost presence of Neanderthals (Photo: Michael Bolus)

Out of Africa Again: Anatomically Modern Humans

Unambiguous evidence for the lineage eventually leading to anatomically modern humans (AMH) comes exclusively from Africa (for an overview, see Bräuer (2008); "▶ Origin of Modern Humans," Vol. 3). According to Günter Bräuer, a long line of evolution becomes apparent on that continent starting some 600,000 years ago with Early Archaic *H. sapiens* (*sensu* Bräuer; most of these fossils, such as Bodo, Ndutu, and Kabwe/Broken Hill, are included by Stringer (2012) and Rightmire (2009) in *H. heidelbergensis*), followed by Late Archaic *Homo sapiens* (*sensu* Bräuer; some of these fossils, such as Florisbad, Laetoli 18, and Irhoud 1 and 2, are included by Rightmire (2009) in a "Florisbad group" of Middle Pleistocene African hominins). First fossils of anatomically modern *H. sapiens* have been found in Ethiopia in the sites of Omo Kibish (McDougall et al. 2005) and Herto (White et al. 2003), with ages of about 195,000 and 160,000 years BP, respectively. These humans produced Middle Stone Age industries with Acheulean elements. Later fossils from Africa include, among others, those from Singa (Sudan), Mumba (Tanzania), Klasies River Mouth, and Border Cave (both South Africa).

Asia

The exact date when AMH left Africa for the first time, often called the "Out of Africa II" movement, remains as unclear as the exact dispersal route(s). The oldest

AMH fossils outside Africa have been found in burials from two caves in Israel: Skhūl in the Carmel Mountains and Qafzeh near Nazareth. These fossils have ages of about 90–100,000 BP, making them the oldest burials known so far. At the same time, these finds mean that there is a temporal gap of about 100,000 years between the oldest AMH fossils from Africa and those from outside Africa. The AMH from Skhūl and Qafzeh both produced Middle Paleolithic assemblages similar to the ones contemporaneous Neanderthals produced in Europe, which shows that biological evolution does not necessarily run parallel with cultural evolution.

After the Skhūl and Qafzeh people, only Neanderthals seem to have settled the Near East for several tens of thousands of years. Coming from the site of Ksar Akil in Lebanon, the next AMH in that region are no older than about 42,000 years and seem to represent another dispersal wave of AMH out of Africa (Douka et al. 2013). These fossils have been found within Initial and Early Upper Paleolithic contexts which clearly differ from the European Aurignacian to be discussed below.

Due to the overall weak fossil record, no clear dispersal route of AMH from eastern Africa (or southern Africa, since genetic evidence seems to indicate a southern African origin for AMH; Henn et al. 2011) can be traced to the Levant. Due to its intermediate geographic position between southern and eastern Africa on the one hand and the Levant on the other, the Egyptian site of Taramsa, which has yielded a probable AMH burial from Middle Paleolithic context (Van Peer et al. 2010), may indicate movements of AMH along the Nile Valley. The burial, however, is dated to about 68,000 BP, so that it is much younger than the earliest AMH fossils from the Levant.

Whether the site of Jebel Faya in the United Arab Emirates (Armitage et al. 2011) falls into the temporal gap remains to be proven. The oldest assemblage of the site dates to about 125,000 BP. Unfortunately, the site has not yielded any human remains so far, but comparisons of the lithic artifacts show similarities with contemporaneous African Middle Stone Age assemblages that are definitely produced by AMH, whereas the site seems to lie outside the Neanderthal range. Given this, Jebel Faya could provide evidence for an expansion of AMH into Arabia earlier than the burials from Skhūl and Qafzeh.

Theoretically, even an independent evolution of AMH in the Near East or in other parts of Asia cannot completely be ruled out, but a record of archaic *H. sapiens* fossils, transitional groups, and early AMH cannot be put together for this region the way it was for Africa. The phylogenetic position of the Zhirendong fossils from South China is still under discussion, and the same is true for the exact ages of other earlier Late Pleistocene human fossils from both continental and insular regions of East Asia (Kaifu and Fujita 2012). With an age of about 40,000 years, the AMH skeleton from Tianyuan Cave in North China (Shang et al. 2007) ranks among the oldest securely dated AMH remains from eastern Eurasia.

The colonization of southern Asia apparently did not happen before the “supereruption” of the Mount Toba volcano on Sumatra (ca. 74,000 years ago). Based on archaeological and genetic evidence, a dispersal scenario has recently been published which suggests a coastally oriented dispersal of AMH from eastern Africa to southern Asia (Mellars et al. 2013). Provided this holds true, dispersals of AMH from southern Asia both to eastern Asia and to Sahul are possible.

Sahul

The colonization of Sahul – the landmass which during the last glacial comprised mainland Australia, New Guinea, Tasmania, and some other neighboring islands – was definitely not possible without crossing water; in this it differs from all earlier dispersals of humans. Even with the water level being about 100 m lower than today, the water barrier to be crossed to enter Sahul measured at least 70 km (Balme 2013). Several routes are conceivable by which AMH may have reached the new territory, most probably by boats or rafts (Birdsell 1977), although none of these routes have been definitely proven yet. In any case, Sahul was the first continent to be colonized exclusively by AMH. Sites with the earliest evidence for human presence in Sahul include Malakunanja 2 and Nauwalabila 1 in Arnhem Land with Optically Stimulated Luminescence (OSL) ages of about 53,000 BP, while the famous Lake Mungo burials in New South Wales date to about 41,000 BP (see Davidson 2010). A couple of other sites have also yielded reliable age estimates around 40,000 BP, whereas ages down to more than 100,000 BP could not be verified. It is noteworthy that sites with ages greater than 35,000 BP are not only to be found near the coastal areas but also inland, which indicates that early AMH in Sahul were able to settle very different environments more or less contemporaneously, thus showing a high degree of adaptive capabilities.

Europe

From the dates given, it is evident that the colonization of Sahul took place prior to the colonization of Europe. But in light of new dates and the reanalysis of human fossils, the first presence of anatomically modern humans in Europe has also been dated back. Different routes are imaginable, and since the fossil record for the earliest Europeans is still sparse, it is essential to consider the archaeological record as well.

The site of Üçağızlı Cave I, located on the Mediterranean coast in the Hatay province of south-central Turkey – that is, positioned at the gates of Europe though not, geographically speaking, quite part of it – yielded important data. A multilayered stratigraphy was excavated, with an Initial Upper Paleolithic (IUP) sequence followed by an Early Upper Paleolithic Ahmarian sequence (Kuhn et al. 2009). Both the IUP and the Ahmarian yielded teeth attributed to AMH, the oldest of them coming from levels with calibrated radiocarbon ages of down to 45,000 calBP (for the dates, see Douka 2013). Archaeologically, the assemblages stand out for a variety of organic tools and personal ornaments coming from all parts of the IUP and Ahmarian sequence.

Recently, two teeth from Grotta del Cavallo (Italy), found in an Uluzzian context, have been reanalyzed (Benazzi et al. 2011). This reanalysis shows them to be from AMH, and not from Neanderthals as supposed earlier. New chronometric data obtained from associated shell beads give (calibrated and modeled) ages of 43–45,000 calBP, making the Cavallo teeth the oldest known European AMH. These fossils have about the same age as the oldest AMH teeth from Üçağızlı. The Uluzzian, in which the Cavallo teeth were found, belongs to the so-called transitional industries, which combine elements of the Middle Paleolithic and the Upper Paleolithic. Since the term "transitional industries" is somewhat misleading, insofar as it implies that one techno-complex (Middle Paleolithic) developed into another (Upper Paleolithic), assemblages of this kind, though still bearing some Middle Paleolithic characters, might more neutrally be termed Initial Upper Paleolithic (IUP). It should be noted, however, that IUP assemblages such as the Uluzzian, the IUP of Üçağızlı, and others differ considerably from each other and should not be attributed to one and the same dispersal wave of AMH into Europe.

The problem of assigning all "transitional industries" jointly to either AMH or Neanderthals is illustrated by the Châtelperronian techno-complex, distributed in larger parts of France and small parts of Spain. Despite ongoing controversy (see, e.g., Bailey and Hublin 2006 and Bar-Yosef and Bordes 2010; Higham et al. 2010), it seems that this techno-complex was created by Neanderthals, whereas, as just mentioned, the Uluzzian was produced by AMH. Both the Châtelperronian and the Uluzzian stand out for the fact that some of the assemblages have yielded bone tools as well as personal ornaments (White 2001; d'Errico et al. 2003; Benazzi et al. 2011). In most cases, the presence of personal ornaments in an assemblage is regarded as a "modern" trait. That is why there is vivid discussion over the notion, advocated by some scientists, that the creators of the Châtelperronian, assuming they were Neanderthals, had been acculturated by incoming AMH (e.g., Mellars 1989). The alternative, argued for by other researchers, is that the Neanderthals themselves had the capability to produce personal ornaments, without any contacts with AMH (e.g., Zilhão 2007). The dispute remains unresolved.

For still another IUP complex, the Bohunician from eastern-central Europe, an authorship of AMH, has been suggested for reasons of lithic technology, which to some extent resembles that of the Ahmarian from the Near East (Škrdla 2003). This suggested authorship, however, remains to be confirmed, since new Thermoluminescence (TL) dates place the Bohunician-type site Brno-Bohunice (Czech Republic) at about 48,000 BP (Richter et al. 2008) – which would imply a much earlier presence of AMH in Europe than previously thought. Unfortunately, no human fossils have been found in a Bohunician context.

Some of the oldest AMH fossils from Europe have either been found without any archaeological context, such as those from Peştera cu Oase in Romania (Zilhão et al. 2007), or with unclear context, such as the maxilla from Kent's Cavern in England (Higham et al. 2011). While for Kent's Cavern calibrated ages of 43–42,000 calBP were obtained from faunal remains (which need not necessarily stem from direct association with the fossil), direct dating of the Oase 1 mandible

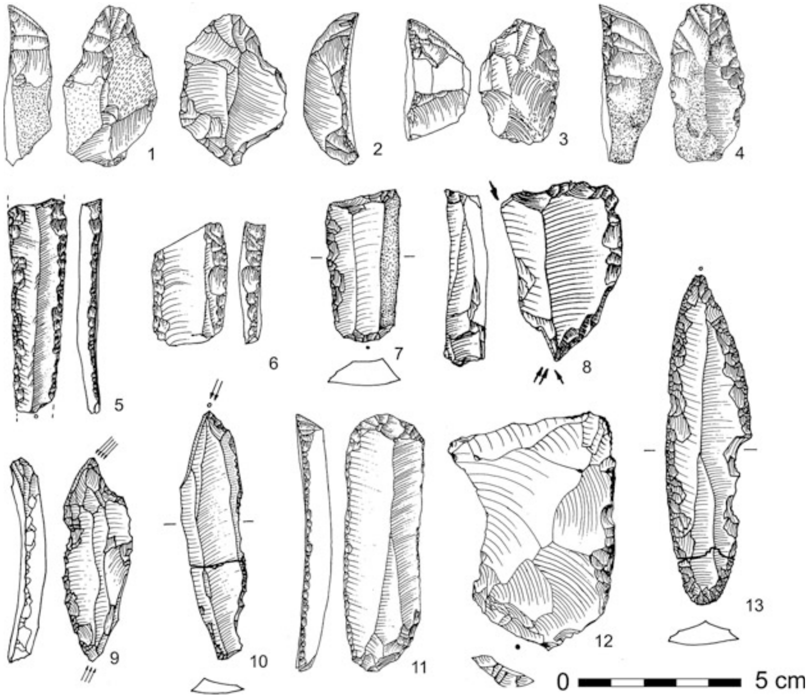


Fig. 5 Stone tools from Aurignacian sites in the Swabian Jura, southwestern Germany. *1*, *2* nosed end scrapers; *3*,*4* carinated end scrapers; *5*,*6* laterally retouched blades; *7* truncated blade; *8–10* burins; *11* end scraper; *12* knifelike flake with lateral retouch and faceted platform remnant; *13* pointed blade (*Spitzklinge*) (After Bolus 2011)

has yielded calibrated radiocarbon ages of 40–38,000 calBP. Looking further to the east of Europe, the Russian site of Kostenki XIV in the Don region yielded two AMH teeth with an Initial or Early Upper Paleolithic assemblage dated to (calibrated) 40–36,000 calBP (Sinitsyn and Hoffecker 2006). The fossils mentioned, even those without clear archaeological context, confirm a rapid dispersal of modern humans across the continent from east to west before the disappearance of Neanderthals.

The archaeological record from early Upper Paleolithic sites in Europe without human fossils adds to this picture, though at first glance the general rarity of human fossils from that time period seems problematic. The Aurignacian is the first fully Upper Paleolithic techno-complex to be present in larger parts of Europe (Fig. 5). Roughly speaking, it can be found from the Don region in the east to the Atlantic coast in the west, though regional differences cannot be ignored. The Aurignacian sensu stricto seems to be an indigenous European techno-complex (Bolus 2004).

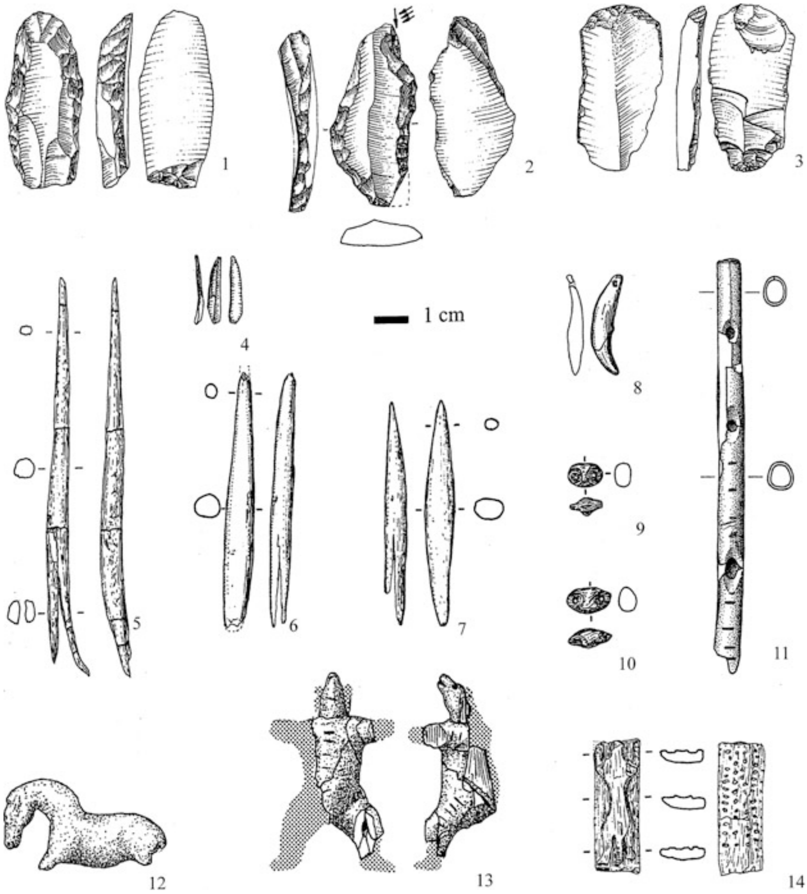


Fig. 6 Stone and organic tools, personal ornaments, art objects, and a musical instrument from Aurignacian sites in the Swabian Aurignacian of southwestern Germany. *1* end scraper; *2* busked burin; *3* splintered piece; *4* Dufour bladelet; *5–7* split-based antler points; *8* perforated fox canine; *9–10* double-perforated ivory beads; *11* bone flute; *12–14* ivory figurines (After Bolus 2011)

The oldest known Aurignacian assemblage comes from archaeological horizon III of the Geißenklösterle Cave in the Swabian Jura of southwestern Germany, with calibrated and modeled ages of down to 43,000 calBP (Higham et al. 2012). Another cave site from the Swabian Jura, Hohle Fels, less than 3 km away from Geißenklösterle, yielded only slightly younger ages from the lowest part of the Aurignacian sequence (Conard 2009). Both sites stand out for their variety of personal ornaments, figural artworks, and musical instruments (Fig. 6). With the ages mentioned, these objects range among the oldest examples of their kinds and thus of what might be called cultural or behavioral modernity (for a definition, see Conard 2008; (see Haidle, chapter "▶ Modeling the Past: Archaeology," Vol. 1 and

Conard, chapter "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," Vol. 3).

Assemblages of similar ages can be found in Bavaria and in Lower Austria. But while the assemblage from layer 2 of Willendorf II in Lower Austria, dated older than 40,000 BP, can only be attributed to an unspecific Early Upper Paleolithic, layer 3 of the same site, which yielded ages around 39,000 BP, clearly belongs to the Aurignacian (Nigst and Haesaerts 2012).

These sites in the Swabian Jura and in Lower Austria are in full accordance with the "Danube Corridor" hypothesis, which states that groups of AMS entered central Europe following the Danube Valley (Conard and Bolus 2003) and from there dispersed further to the west and northwest.

Calibrated age estimates for the oldest French Aurignacian strengthen the argument, since they are somewhat younger than those for the Swabian sites. The oldest French Aurignacian sensu stricto comes from Abri Pataud in the Dordogne and is younger by about 2,000 years than the oldest Aurignacian from Geißenklösterle (Higham et al. 2012). Assuming a high dispersal speed, these dates would be well compatible with the scenario of the "Danube Corridor."

Unfortunately, neither Geißenklösterle nor Hohle Fels nor any other early Aurignacian sites of similar age have yielded human fossil remains. The oldest example from secure Aurignacian context comes from the site of La Quina-Aval in France, with a calibrated age of about 38,000 calBP (Verna et al. 2012). Other, somewhat younger sites include Brassempouy and Les Rois, both in France as well. Since in every case when human remains have been found in secure Aurignacian context, the remains were identified as AMH (see also Bailey et al. 2009), and since the Aurignacian assemblages from Geißenklösterle and Hohle Fels represent full Aurignacian assemblages, it seems plausible to see AMH as the hominins responsible for the Swabian Aurignacian in particular and, by extension, for the European Aurignacian in general. This line of argument offers an illustration of how archaeology can provide valuable information on the dispersal of early AMH within Europe where human fossils are lacking.

From the northern Mediterranean region, a similar techno-complex is known: the archaic Aurignacian, also called Proto-Aurignacian or Fumanian. It is not necessary here to discuss the differences and the similarities with the Aurignacian sensu stricto. In all sites where both techno-complexes are present, the archaic Aurignacian underlies the Aurignacian sensu stricto. This does not mean, however, that the archaic Aurignacian is automatically older. Instead, the oldest archaic Aurignacian sites from Fumane and Riparo Mochi in Italy, Abric Romaní in Spain, and Arcy-sur-Cure and Les Cottés in France have yielded calibrated radiocarbon ages between about 42,000 and 40,000 calBP (Higham et al. 2012), thus being slightly younger than the oldest Geißenklösterle dates and contemporaneous with other dates for the Aurignacian sensu stricto. Uncalibrated ages of down to 40–39,000 BP have been obtained for archaic Aurignacian assemblages from northeastern Spain (Arbreda and Reclau Viver: Soler Subils et al. 2008).

The human fossil record for the archaic Aurignacian is even worse than it is for the Aurignacian sensu stricto. Either there are no fossils from the assemblages at all, or the fossils are not unambiguously from the archaic Aurignacian levels, or they are not attributable to specific hominins. Hence, though the suggestion to attribute the archaic Aurignacian to AMH is the most plausible one, it is just that – a suggestion.

Nevertheless, this question is of particular importance since, on the assumption that AMH were responsible for the assemblages of archaic Aurignacian type, those assemblages would be indicative of another dispersal route of early AMH into and through Europe – a route which did not run along the Danube Valley but along the northern Mediterranean coast and from there, as the sites of Arcy-sur-Cure in Burgundy and Les Cottés in Auvergne show, further inland.

This returns us to the question from where and how AMH came into Europe. The first dispersal wave of AMH out of Africa, about 100,000 years ago, does not seem to have reached Europe. The fossils from Üçağızlı at the gates of Europe as well as the oldest AMH fossils found in Europe, and the European archaeological record leave a clear temporal gap between the earliest AMH presence outside Africa – in the Near East and even in Sahul – and the colonization of Europe. The scenario of a second wave of dispersal of AMH into Europe from Africa, crossing the Levantine Corridor, is put into question by the relatively young dates for the Ksar Akil fossils. The Aurignacian sensu stricto as well as the archaic Aurignacian had already been fully established at the time of the Initial/Early Upper Paleolithic in the Near East. On the other hand, further research is needed to strengthen the possibility of a dispersal of AMH from East and Central Asia into Europe. The oldest securely dated AMH fossils from East Asia, all found in Early Upper Paleolithic contexts but in neither case within Aurignacian contexts, do not seem to be older than the oldest AMH fossils from Europe.

This leads back to the archaeological evidence and the suggestion of a genuine European origin of both the archaic Aurignacian and the Aurignacian sensu stricto. Based on the archaeological and the fossil evidence, a scenario is imaginable where AMH entered Europe from the Near East and/or Central Asia moving both through the Danube Corridor and along the northern Mediterranean rim, finally reaching the western and northwestern ends of the continent. It seems that the earliest colonizers of Europe had some sort of Initial or Early Upper Paleolithic industry with them, but no Aurignacian. During their spread across Europe, numerous innovations evolved within the material culture, and most probably changes in the social/behavioral realm appeared as well. It is noteworthy that the earliest evidence for the full development of these features comes from the Swabian Jura in southwestern Germany. This leads to the hypothesis that early AMH entered Europe showing some, but not all, characteristics of fully modern behavior. These were developed somewhere in (central) Europe with the Aurignacian sensu stricto and along the northern Mediterranean rim with the archaic Aurignacian. At least two different routes can be traced following the archaeological record; what it confirms very

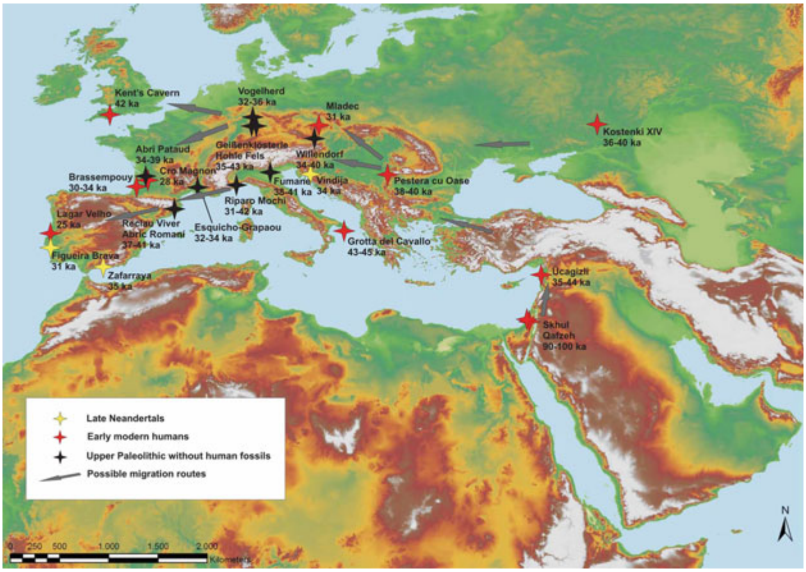


Fig. 7 Sites with late Neanderthal fossils, with early AMH fossils, with early Upper Paleolithic assemblages (but without human fossils), and possible dispersal routes of AMH into and through Europe

clearly is that AMH, once having entered Europe, spread rapidly through the continent (Fig. 7).

The New World

The last major dispersal steps were made when at the end of the last glacial, about 15–14,000 years ago, AMH started to colonize the Americas until, finally, they had entered most parts of the habitable world. From where exactly the colonization of the New World took place is still open to debate (see Davidson (2013) and the references given therein) and shall not be further discussed here.

Third Party: The Denisovans

Until about a decade ago, Neanderthals and AMH were the only known hominins during what is archaeologically defined as the late Middle Paleolithic and Upper Paleolithic. The discoveries from Liang Bua Cave and other sites on Flores, Indonesia, however, demonstrated that it is better to be cautious with preconceptions. The exact taxonomic position of the Liang Bua fossils is still under debate (see Aiello, chapter "▶ *Homo floresiensis*," Vol. 3). The implications of these fossils and of stone artifacts from sites such as Mata Menge on Flores, with a possible age of down to 0.8 million years (Brumm et al. 2010), shall not be discussed here.

Fig. 8 Denisova Cave in the Russian Altai Mountains. A Neanderthal pedal phalanx as well as fossils of a new hominin group, the Denisovans, have been found here (Photo: Michael Bolus)

Another discovery of the recent past must at least be touched on, though the various implications of this discovery are not yet fully understood. In 2010, geneticists announced the discovery of a new, hitherto unknown human group (Krause et al. 2010; Reich et al. 2010). A human finger phalanx excavated in the Denisova Cave in the Russian Altai (Fig. 8) in 2008 yielded an mtDNA sequence belonging neither to Neanderthals nor to AMH. According to the site where the bone had been found, the new lineage was named the Denisovans. However, geneticists cautioned that it might be premature to apply "any formal Linnaean taxonomic designation that would indicate species or subspecies status for either Neanderthals or Denisovans" (Reich et al. 2010, p. 1059). Until now the new hominin group is only known from the phalanx mentioned and two molars, all excavated at Denisova Cave. In the meantime, a draft nuclear genome sequence has been retrieved from the phalanx. It "revealed that Denisovans are a sister group to Neandertals, with the Denisovan nuclear genome sequence falling outside Neandertal genetic diversity, which suggests an independent population history that differs from that of Neandertals. Also, whereas a genetic contribution from Neandertal to the present-day human gene pool is present in all populations outside Africa, a contribution from Denisovans is found exclusively in island Southeast Asia and Oceania" (Meyer et al. 2012). Further genetic data suggest that Denisovan gene flow occurred in Southeast Asia and not mainland East Asia. This leads to the conclusion that archaic Denisovans "must have lived over an extraordinarily broad geographic and ecological range, from Siberia to tropical Asia" (Reich et al. 2011, p. 516). Most recently, a mitochondrial genome sequence gained from a hominin femur from Sima de los Huesos has revealed a close relationship to the lineage leading to the mitochondrial genomes of Denisovans (Meyer et al. 2014).

It is obvious that further research, in particular analysis of more fossils belonging to the Denisovans, is needed to better understand the dispersals of these newly discovered hominins.

Three or Four Different Hominin Lineages: Did They Meet?

In light of the possibility that at least three (or perhaps four, including the Liang Bua fossils) different hominin lineages existed during the later Middle Paleolithic and the Upper Paleolithic, the question may be raised whether these different hominins met during their dispersals or not. From an archaeological point of view, the situation is still not clear. As far as the so-called transitional industries between Middle and Upper Paleolithic are concerned, so far no unambiguous proof has been established that they are the result of contacts between Neanderthals and AMH. The possible case of the Châtelperronian has been discussed above. The fact that up to 4 % of Neanderthal DNA has been detected in the AMH genome, however, is proof of interbreeding, and the fact that this Neanderthal DNA has been found in all living non-African AMH while it is lacking in all Africans demonstrates that this interbreeding must have occurred outside of the African continent. Most probably, it happened in the Near East, but the exact date of the admixture is still open to discussion (Green et al. 2010).

AMH also mixed with Denisovans, most probably in Southeast Asia (Reich et al. 2011). And very recent genetic data suggest an even more complex scenario of admixtures. The Denisovans clearly interbred not only with AMH but also with Neanderthals, most probably in the Middle East. Finally, the genetic results hint at the possibility that Denisovans also mixed with still another, more ancient hominin (Prüfer et al. 2014). If so, this would open a completely new chapter of human history and dispersals.

Conclusion

At the moment, it seems most probable that representatives of the genus *Homo* were the first hominins to leave their African home continent. In contrast, for the genera *Australopithecus* and *Paranthropus*, only dispersals within Africa can be traced. The dispersals of *Homo* out of Africa happened during several waves over a time span of about 1 million years. The first humans outside of Africa, with an age of about 1.8 million years, have been found in Dmanisi in the Georgian Caucasus. Only slightly younger evidence from Southeastern and eastern Asia belongs to the same first wave of expansion. Sites and fossils in the Levantine Corridor with an age of 1.5–1.2 million years may be late witnesses of the same wave or early witnesses of one of the next. The Levantine Corridor is regarded as one of the major dispersal routes for early humans at that time. A southern route crossing the Arabian

Peninsula has also been discussed, but archaeological and fossil evidence for that early time is still lacking for that region.

The earliest material culture of humankind, with an age of around 2.6 million years, is named Oldowan. The first human fossils outside of Africa, although considerably younger, are still associated with this techno-complex. Even humans belonging to later expansion waves, such as those from Atapuerca (Sima del Elefante and Gran Dolina), still produced Oldowan tools. In Africa, a new technological tradition, the Acheulean, started to evolve some 1.8 million years ago. The Acheulean seems to have reached southern Asia much earlier than Europe, where the earliest secure appearances are no older than 700–600,000 years, while evidence from East Asia and the Near East is somewhat older. The European fossils assigned to *H. heidelbergensis* may be representatives of one of the last (if not the last) expansion wave(s) of archaic hominins out of Africa.

The Neanderthals, genuine European hominins, evolved probably out of later representatives of *H. heidelbergensis*/archaic *H. sapiens*. They repeatedly left their core area in southeastern and southern Europe to move into areas of temporary occurrences. During the last glacial period, they started their dispersal "out of Europe" and finally reached an area as far away from their original core area as the Russian Altai Mountains in southern Siberia.

While Neanderthals inhabited Europe and later moved out of Europe, AMH evolved in Africa nearly 200,000 years ago. First AMH fossils outside of Africa with an age of about 100,000 years have been found in the Levantine Corridor, but there is archaeological evidence for an even earlier presence of AMH in the Arabian Peninsula. A considerable temporal gap exists between these appearances and the next evidence for AMH outside of Africa. With the Arabian Peninsula serving as some sort of bridge, it seems plausible that early AMH followed a southern route until finally reaching Sahul some 50,000 years ago.

The colonization of Europe started no earlier than about 45,000 years ago. Only slightly later, by about 43,000 years ago, a new techno-complex, the Aurignacian, evolved in Europe and gradually spread over larger parts of the continent. The archaeological evidence suggests a dispersal of early AMH through the Danube Corridor. Another dispersal route of early AMH is suggested by sites around the northern Mediterranean rim which are attributed to the archaic Aurignacian and which are more or less contemporaneous with the Aurignacian sites. With a broad variety of organic tools, personal ornaments, figurative art, and musical instruments, the makers of the early Aurignacian and archaic Aurignacian, most probably AMH, show the full package of what is called fully modern behavior. Once in Europe, AMH spread rapidly across the continent.

While the archaeological evidence is not that clear, genetic data show that AMH mixed both with Neanderthals and with a recently discovered, new hominin group, the Denisovans, which in turn also mixed with Neanderthals.

At about 15–14,000 years ago, AMH finally started to colonize the New World.

Today, much is known about adaptations, traces, frontiers, and new territories during the several repeated dispersal waves of early hominins. But it is also clear, as evidenced by the ongoing discovery of surprising finds, such as the Liang Bua fossils from Flores, the Denisovans, and yet another possible hominin lineage, that researchers are far from understanding the whole scenario of inter- and intracontinental dispersals of early humans.

Cross-References

- ▶ Chronometric Methods in Paleoanthropology
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ Defining *Homo erectus*
- ▶ Genetics and Paleoanthropology
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Later Middle Pleistocene *Homo*
- ▶ Modeling the Past: Archaeology
- ▶ Neanderthals and Their Contemporaries
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- ▶ Overview of Paleolithic Archaeology
- ▶ The Earliest Putative *Homo* Fossils
- ▶ The Miocene Hominoids and the Earliest Putative Hominids
- ▶ The Species and Diversity of Australopiths
- ▶ Zoogeography: Primate and Early Hominin Distribution and Migration Patterns

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The Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia

Christy G. Turner II and G. Richard Scott

Contents

Abstract

This chapter uses dental morphology to make inferences about how the New World was first colonized. The major emphasis is on the initial Macro-Indian migration based on dental traits observed in Paleo-Indian, Archaic, and more recent prehistoric crania. The major results are as follows: (1) Arctic and Subarctic

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Christy G. Turner II passed away on July 27, 2013. This chapter has subsequently been updated by his coauthor.

C.G. Turner II
Deceased. Formerly at School of Human Evolution and Social Change, Arizona State University, Tempe, AZ, USA

G.R. Scott (✉)
Department of Anthropology, University of Nevada, Reno, NV, USA
e-mail: grscott@unr.edu

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native dentitions differ enough from those of Macro-Indians to indicate separate migrations. (2) Clustered MMD values show three Macro-Indian branches of North Americans, South Americans, and mixed North and South. (3) There is no marked branching depth for these three dental divisions, which fits the hypothesis of a single rapid Paleo-Indian colonization event. (4) The minimally divergent North and South American dental divisions are most likely the microevolutionary result of dispersal-dependent population structure and lineage effects. (5) No genetic bottlenecking can be identified at Panama. (6) The small amount of New World internal dental divergence favors colonization of South America soon after the settlement of North America. (7) There are no obvious clines, frequency trends, or geographic groupings for individual dental traits. This suggests little or no selection and that after leaving Siberia, population size increased sufficiently to limit genetic drift. (8) There is no sign of any Old World or Oceanic dental pattern other than Northeast Asian Sinodonty. All things considered, including New World and Siberian linguistics, archaeology, genetics, route considerations, and relevant natural history, dental analysis supports the Late Pleistocene ice-free corridor, Clovis or epi-Clovis settlement hypothesis, and the Greenberg Amerind or Macro-Indian language evolution model.

Introduction

This chapter reviews the dental morphological evidence for the pre-Columbian colonization of the New World. This evidence, in conjunction with genetic information, is used to challenge colonization scenarios based on measurements of prehistoric skulls. There are two main anthropological questions for which answers have been sought using the variation of New World dental morphology and comparative information from Old World and Pacific basin populations. First, how many colonizing migrations can be postulated on the basis of New World dental variation? To answer this question, analysts have tried to determine if there are any dental correspondences with modern or ancient New World culture areas (yes), environmental types (no; however, Jantz et al. 1992 found that anthropometric variation was correlated with geography), or linguistic families (yes) (Greenberg et al. 1986). These findings suggest that New World dental variation is more closely linked to ethnicity (i.e., migration) than to environment (natural selection or physiological adaptation). Roughly put, dental variation is strongly caused by nature, whereas cranial variation has a significant nurture component (Kohn 1991, p. 273) notes that "environmental factors contribute a significant amount to the observed variability in craniofacial morphology and growth"). Because of linguistic and ethnic correspondences with dentition, Arctic and western Subarctic dental variation is most parsimoniously interpreted as due to two migrations of people dentally differentiated to a slight degree from an earlier migration (Clovis or epi-Clovis). All three inferred migrant groups exhibit minor variants of the Sinodont dental pattern and, as such, are closely related and share a common Northeast Asian ancestor sometime in the relatively recent past. Presumably, each originated in different geogenetic regions of Northeastern Asia (Turner 1985) after separating from the common ancestral stock that presumably lived further to the south, say, central China. As will be shown, the earliest colonizers must have given rise to all modern North and South American populations except for Arctic and Subarctic groups. This first migrant group is referred to as Macro-Indian or Amerind, linguistic names (Ruhlen 2000), and Paleo-Indian or Clovis, synonyms used by archaeologists (Haynes 1987). The term epi-Clovis has been recently proposed to denote the Late Pleistocene ancestral cultural condition in Beringia prior to the development of the fluted points that are the hallmark of the Clovis big-game hunters (Turner 2002). Another name used in Alaska to denote epi-Clovis is Nenana complex (Hoffecker et al. 1993). In addition to the just-cited articles, other major reviews of the archaeological evidence for the peopling of the Americas can be found in Carlson (1991), Fiedel (2004), Haynes (2002a, which contains an immense bibliography, 2002b), Hoffecker and Elias (2003), Madsen (2004), Meltzer (1993), Rogers et al. (1992), West (1996), Yesner (2001), Yesner and Pearson (2002), Graf et al. (2013), and many others. The emphasis here is on the importance of archaeology and archaeologically derived teeth since both provide direct diachronic evidence for human biocultural prehistory.

In the Old World, the Sinodont dental pattern occurs in modern and prehistoric Northeast Asians of China, Tibet, Mongolia, post-Jomon Japan, Korea, and eastern Siberia (Hanihara 1968; Zoubov and Haldeyeva 1979; Hanihara 1991; Scott and Turner 1997). In contrast, Late Pleistocene and recent peoples of mainland and island Southeast Asia (Thailand, Indonesia, Borneo, Philippines, Taiwan, Jomon Japan, etc.), as well as Polynesians, Micronesians, and early Sri Lankans, possess a dental pattern called Sundadonty, which is simpler and retains more of the character of a hypothesized earlier pattern (proto-Sundadonty) than does the more specialized Sinodonty (Turner 1983, 1990a; Scott and Turner 1997). Modern and recent Europeans, as well as the earlier Cro-Magnons, possess a simplified dental pattern, which is similar to that found in modern India, North Africa, and western and central Asia (Irish 1993; Haeussler 1996; Hawkey 1998). The simplest of modern human dental patterns is found in Europe (Scott et al. 2013). It more closely resembles the dental pattern of modern Africans and Australians than Sinodonty.

The second question involves claims using controversial archaeological and craniometric evidence that proposes the New World was initially colonized by a pre-Clovis, Sundadont population that was less Mongoloid cranially than modern Indians. These claims presume an earlier entry into the New World than the classic Clovis-first model. Claims for pre-Clovis range widely, from 15,000 to more than 50,000 years BP.

To put the peopling of the New World into a broad framework of dental pattern evolution, a phylogenetic reconstruction is offered that seems to have the best general concordance with other lines of evidence derived from archaeology, linguistics, genetics, and natural history. In this context, dental pattern refers to a standardized set of independent discrete crown and root morphological traits whose occurrence (presence or absence) and expression (small, moderate, large, very large; shape variation; etc.) in one major geographic region, such as Northeast Asia, differ considerably from what is found in other major natural regions, such as Europe (cf. Scott et al. 2013). The authentication of these patterns has been based on repeated dental sampling of the geographic regions, which produces trait frequencies like those originally used to define the regional patterns. On dental grounds, prehistoric Europeans and Africans are excluded as having anything to do with the peopling of the New World until the Christian era. Similarly, teeth indicate that peoples of Oceania and Southeast Asia played no role in the colonization of the New World. Long before Siberians reached Alaska, human populations had evolved their major modern dental patterns. Scott and Turner (1997) identify these as belonging to five groups: Africa south of the Sahara, western Eurasia (Europe, Middle East, North Africa, India), Sahul-Pacific (Australia, New Guinea, Melanesia), Sunda-Pacific (mainland and insular Southeast Asia, Polynesia, Micronesia), and Sino-American (Northeast Asia and the Americas). Finally, all claims for an autochthonous creation of Native Americans, as based on some religious beliefs, as well as on flawed reasoning, are excluded from consideration (Tyler 1998).

To put the peopling of the New World into a broader human evolutionary context, it is necessary to first consider what is known about human evolution in Asia during the Upper Pleistocene. Sometime before 50,000 BP, there were anatomically modern humans living in Southeast Asia, although among complete specimens only the south China Liujiang skull may be this old or older (Pope 1992, p. 275). However, the 50,000 BP date approximates the earliest archaeological appearance of human-made stone artifacts in Australia (Roberts et al. 1994). All human skeletal remains found in Australia, some dating as far back in time as 30,000 BP, are anatomically modern. Australia could only have been colonized from Southeast Asia, at a few locations along the route and only with the aid of some form of watercraft. Early Southeast Asians and Australian colonists are hypothesized to have possessed a dental pattern similar to that of modern Australians. Turner (1992c) has called this hypothetical pattern proto-Sundadonty, which was estimated by averaging the dental trait frequencies obtained from archaeologically and ethnographically derived skeletal samples collected in several localities throughout Australia. In their early terrestrial and oceanic dispersal eastward out of Southeast Asia, proto-Sundadonts, in time, became ethnic Melanesians and Australians. Their dental pattern is much like that found in modern and recent Southeast Asians as well as modern sub-Saharan Africans, suggesting proto-Sundadonty and the African dental pattern were derived from an as yet unidentified common ancestral pattern. Before the end of the Pleistocene 10,000 years ago, Southeast Asian teeth had evolved into the slightly more specialized Sundadont pattern as part of the general drift toward dental complexity in eastern Eurasia, in contrast to the Late Pleistocene drift toward increased simplicity in western Eurasia. The areal extent of Sundadonty increased with the northward coastal expansion of these modern humans into Taiwan and Jomon Japan, where Sundadonty remains to the present day in unadmixed Taiwan aborigines and the Ainu of northern Japan. In the more interior part of the East Asian mainland, probably north China, Sundadonty evolved into the more complex and specialized Sinodont pattern. In time, nomadic groups possessing Sinodonty expanded into Mongolia, eastern Siberia, and eventually the New World. In the later Holocene, Southeast Asians traveled the Pacific by large sailing watercraft to become island populations of Polynesians and Micronesians, retaining their Sundadont pattern. Thus, all around the Pacific basin, there are three distinctive dental morphological patterns: proto-Sundadonty (Sahulland: Australia and Melanesia), Sundadonty (Sundaland: mainland and island Southeast Asia; island East Asia), and Sinodonty (Sino-America). At least 50,000 years are involved in the evolution of this Asian-Pacific dental patterning. In terms of time involving only several thousands of years, these patterns are evolutionarily quite stable and remarkably consistent in ethnically related groups living in strongly dissimilar ecological settings. Such demonstrable stability is part of what makes dental morphology eminently useful for evaluating long-term diachronic and synchronic affinities, population origins, and microevolutionary processes.

New World Arctic and Subarctic Dental Variation

While all New World teeth conform to the Sinodont dental pattern, first defined on the basis of prehistoric Chinese teeth, those of Arctic and Subarctic Eskimos, Aleuts, and speakers of Na-Dene languages differ slightly from those of Macro-Indians (Scott and Turner 1997, 2008). For example, pronounced upper incisor shoveling is less frequent in Eskimos and Aleuts than it is in Macro-Indians. It tends to be intermediate in Subarctic Indians. Eskimos and Aleuts have greater frequencies of three-rooted lower first molars than do Macro-Indians, while western Subarctic tribes are intermediate. When the three New World groups – (1) American Arctic, (2) Northwest North America, and (3) North and South America – were graphed for mean trait frequencies and standard errors of 23 crown and root traits, ten of the traits show the intermediate nature of Northwest North America, viz., Eskimo-Aleuts and American Indians in general, while 11 traits showed similar frequencies across the three groups (Scott and Turner 1997). The only two traits that failed to exhibit intermediary or similarity were incisor interruption grooves and odontomes, but the differences were not dramatic in either instance. The intermediacy of Northwest North American natives was addressed by Scott and Turner (2008) who suggest it is likely due to ancient gene flow between groups ancestral to modern Na-Dene and Algonquian speakers.

Multivariate and univariate analyses and comparisons show that all New World groups are dentally more like Northeast Asians than any other major geographic group in the world. Nevertheless, the teeth of New World Arctic and Subarctic peoples are generally more like those of Northeast Asians than are the Macro-Indian populations, which, as archaeological evidence suggests, means that the Macro-Indian colonization occurred before or separated from that of the modern Arctic and Subarctic populations. It has been inferred that the concordances between New World archaeological groups and biological populations likely are big-game hunting Clovis fluted point makers = Paleo-Indian Sinodonts; smaller-game hunting Paleo-Arctic biface and microblade makers = Na-Dene/Greater Northwest Coast Sinodonts; and Maritime Anangula blade makers = Aleut-Eskimo

Sinodonts. What holds these concordances together are their individual geographic distributions for artifact types, dental divisions, and language families.

Macro-Indian Dental Variation

Comparative analyses of Native American dentitions by Haeussler and Turner (1992), Hanihara (1979), Perzigian (1984), Powell (1993), Scott (1973, 1991), Scott et al. (1983, 1988), and Turner (1983, 1985, 1986, 1990a, 1992a, b, 1993, 2002), as well as contemporary genetic studies by Callegari-Jacques et al. (1993), Cavalli-Sforza et al. (1988, 1994), Horai et al. (1991), Laughlin and Harper (1988), Stone and Stoneking (1993), Szathmary (1979, 1993), Torroni et al. (1992), and others reviewed herein, and most osteological studies by Alekseev (1979), Kozintsev (1995), Steele and Powell (1992), and Brace et al. (2001) are in good agreement that the ancestors of Native Americans originated in Northeast Asia. However, a few osteological studies are not in full accord with this general inference. Howells' (1989) worldwide craniometric analyses showed male Peruvians and Californians clustering with males from Europe, while his male Arikara Indians clustered with male New Zealand Moriori. Neves and Pucciarelli (1991) argued on multivariate grounds that early South American crania are morphometrically closer to Australians even though their principal component plots show early South Americans equally similar to East Asians and Europeans. Owsley (2013) analyzed Paleo-Indian skulls from the Americas and found they were most similar to and clustered with recent Polynesians. Inasmuch as archaeology (West 1981, 1990; Dillehay and Meltzer 1991; Stanford and Day 1992; Meltzer 1993), linguistics (Greenberg et al. 1986; Greenberg 1990; Greenberg and Ruhlen 1992), and paleo- and neo-geography (Hopkins 1982; Laukhin 1997), as well as dentition, genetics, and most osteology, strongly support a Northeast Asian origin for all Native Americans, the cited craniometric studies are notable exceptions to the Northeast Asian-American anthropological and other correspondences as well as the Sino-American dental correspondences (Scott and Turner 1997). Nevertheless, in recent years there has been a concerted effort to resuscitate the notion of a pre-Clovis occupation of the Americas (Hall 2000; many papers in Graf et al. 2013).

A Brief History of the Pre-Clovis Revival as It Bears on Dental Variation

There has long been disagreement between Americanist scholars who line up with the late Aleš Hrdlička (1925) by arguing that the colonization of the New World was late compared to the amount of human evolution in the Old World, in contrast to scholars who believe there is evidence for much older human occupation in the New World. For example, Krieger (1964) (pre-projectile occupation), Carter (1957) (very ancient occupation), Müller-Beck (1967) (Mousteroid element in Americas), and others posit very early migrations (>20,000 BP) of peoples from the Old to the New World. There have been any number of archaeological claims for pre-Clovis occupation of the New World, but as Meltzer (1993) noted, the claims usually have a "shelf life" of about 5 years. Among modern physical anthropologists, several revivalists of the pre-Clovis and/or non-Mongoloid origins include Neves and Pucciarelli (1991, and several similar articles), Crawford (1992), Lahr and Haydenblit (1995), Steele and Powell (1992), and Owsley (2013).

Lahr and Haydenblit (1995) proposed that Sundadonty was present in a series of South American crania from Patagonia and Tierra del Fuego. In a lengthy review article, Lahr (1995) proposed that either Sinodonty evolved in parallel in Asia and the Americas or there were two migrations ancestral to Native Americans, i.e., a Sundadont group followed by a Sinodont group. Based on a dental morphological analysis of Peruvian and Chilean samples, Sutter (2004) arrived at a similar conclusion. He notes that older samples exhibit dental morphology more in line with the simplified Sundadont pattern, while later groups exhibit the more complex features associated with Sinodonty.

These proposals are inconsistent with dental observations on South Americans. The senior author has never observed a South American series or individual skull that could be considered as having the Sundadont pattern. This includes the Lagoa Santa remains housed in Brazil and those curated in Denmark, as well as Archaic samples from coastal Brazil, Chile, Ecuador, and Peru. The observations of Lahr and Haydenblit on degree of trait expression may have been impacted by dental attrition. Wear most likely caused the underscoring of crown traits that led them to propose the presence of Sundadonty (Burnett et al. 1998). Tooth wear might also have misled Powell and his associates in their observations on small Paleo-Indian samples. The observation of Stojanowski et al. (2013) that some South American samples exhibit root trait frequencies that would not be impacted by crown wear and yet are in line with the Sundadont pattern has not been fully evaluated.

When Steele and Powell (1997) evaluated craniometric data of two ancient skulls from Nevada (Spirit Cave, Pyramid Lake) that dated ca. 9,500 BP, they found that they failed to cluster with any of 22 comparative modern populations. They felt the skulls were more closely aligned with South Asian, Pacific, and Australian populations than with North Asian and recent North American Indians. They concluded that "the studied Paleoindians arrived in the Americas prior to the establishment of the crania shape that is distinctive of recent Northern Asians and North American Indians, and that the colonization of the Americas was more complex than has previously been proposed" (Steele and Powell 1997, p. 218). This contrast was also reported by Jantz and Owsley (2001). Again using craniometric data, they concluded Paleo-Indians were more similar to Polynesians, Europeans, and East Asians than to recent American Indians.

Taken altogether, the form of the Paleo-Indian skull relative to most of the comparative samples is a reflection of not only geogenetic linkages but also sedentism and its related nutritional, growth, health, and activity benefits and stresses. Thus, African samples cluster together (geogenetic linkage) despite both nomadism and sedentism being represented. The same can be said for the European, Northeastern Asian, and Oceanic sets. Given that archaeological remains of Paleo-Indians strongly suggest a nomadic hunting life way, then the cranial differences between Paleo-Indians and recent Native Americans should have been interpreted along economic lines as much as geogenetic. Only in the last sentence of their article do Steele and Powell (1992) remark on the possibility of "adaptational" factors contributing to the cranial differences between Paleo-Indians and recent Native Americans. All but one sentence in this article is clearly aimed at identifying possible "genomic" differences between Paleo-Indians and recent Indians.

It should be noted that Steele and Powell (1992, p. 329) speak of Paleo-Indian crania as not being "classically sinodont in craniofacial appearance. Instead, it differed by appearing as much like modern southern Asians [recall they use this term to refer to Chinese, who have traditionally been classified as Mongoloids] as it did recent North American Indians and northern Asians. In this respect our findings resemble the contentions of previous scholars that the earliest recovered samples were proto-Caucasoid or proto-Mongoloid."

There has never been an analysis carried out to show if there is a relationship between craniofacial morphology and Sinodonty or Sundadonty. Steele and Powell have assumed that vaults, faces, and teeth go together like a hand in a glove. In fact, Sinodonty is found in people whose craniofacial variation includes every shape in South and North America, including robust California Indians, heavy and long-skulled Southwest US Basketmakers, and robust long-headed Archaic crania from Mexico, Brazil, and Chile, to round-headed gracile Southwest Puebloans, Chinese, Japanese, Buriats, and a long list of other long- and round-headed Northeast Asians. As for early Native Americans having been proto-Caucasoids, a notion strongly championed by Birdsell (1951), Harris and Turner (1974) showed that dental morphology was in opposition to such typological thinking.

Genetics and the Peopling of the New World

During the first half of the twentieth century, scholars who investigated issues relating to the settlement of the New World came primarily from archaeology and skeletal biology. During the past 50 years, genetic data have played an increasingly important role in debates on Native American population history. Researchers have applied three different kinds of genetic data to the problem. Initially, focus was on nuclear genetic markers, from red blood cell antigens and serum proteins to red cell enzymes, immunoglobulins, and white blood cell antigens (cf. Mourant 1954; Mourant et al. 1976; Roychoudhury and Nei 1988; Cavalli-Sforza et al. 1994). In the 1980s, a new and different type of genetic marker was used, one derived from the single-stranded DNA of the mitochondria (mtDNA) which was transmitted, with but few exceptions, through maternal lineages (for reviews, see Cann 1988; Long 1993). Finally, in the 1990s, the Y chromosome was sequenced and a surprising variety of interesting polymorphisms emerged (cf. Hammer and Zegura 2002; Jobling et al. 2004).

The literature in the field has expanded at an exponential rate during the past two decades. It is beyond the scope of this review to provide a detailed synthesis of genetic studies. The goal is to highlight some of the results from the three different sorts of genetic data to determine the extent to which the analyses of synchronic genetic data correspond with peopling models based on diachronic dental data.

Nuclear Markers

Around 1950, the nascent field of human genetics started to weigh in on the issue of Native American origins. On that date, W.C. Boyd published his seminal work *Genetics and the Races of Man*. Therein, he utilized available data on three red cell antigen systems (ABO, Rh, MN) to set up a classification of modern human groups. He deemed Native Americans to be sufficiently distinct from other groups to warrant their own racial category. In this regard, he noted that Indians lacked the "r" allele of the Rh system and the A^2 and B alleles of the ABO system, although Eskimos did have a low frequency of B. Indians also showed a relatively high frequency of the M allele and a marked dichotomy in frequencies of the A and O alleles of the ABO system. Populations south of the US-Mexico border showed essentially 100 % O alleles, while some North American groups, in particular Algonquians, Athapaskans, and Eskimo-Aleuts, exhibited high frequencies of the A allele. While similarities to Asian populations were noted (lack of r and A^2), Boyd felt that the high frequency of the M allele and the very low frequency of B were sufficient to distinguish Asian and American "races."

Laughlin (1951) used blood group data along with anthropometric and osteometric comparisons to assess the affinities of Aleut populations. He felt the presence of the B allele indicated Aleuts were closer to Eskimos than Indians. Moreover, he noted that the "B present in the Eskimos is an indication of their recent Asiatic heritage" (Laughlin 1951, p. 119). Throughout his career, Laughlin (1963, 1966) adhered to the notion that there were two major groups in the Americas – American Indians and Aleut-Eskimos. After comparing Native Americans to Siberians for allele frequencies on the ABO and MN systems, Laughlin (1966, p. 473) opined that the "essential affinity of the Eskimo-Aleut stock with Asiatic Mongoloids, rather than with American Indians, is well attested."

With the development of starch gel electrophoresis in the early 1950s, there was a dramatic increase in the number of genetic surveys across the Americas and throughout the world and in the number of genetic systems that became standard markers for population profiles. By the 1970s, the original three RBC antigen standards were complemented by the addition of many more antigen systems and serum proteins (e.g., Diego, P, Duffy, Kell, Kidd, Haptoglobin, Transferrin, Albumin, etc.). By the time of their massive worldwide synthesis, Cavalli-Sforza et al. (1994) were able to tabulate data on 120 nuclear alleles.

Beginning in the 1970s, Szathmary (1979, 1981, 1993, and elsewhere) played an important role in making inferences on long-term population history based on the analysis of Native American gene frequency profiles. One of her early efforts, prepared with Nancy Ossenberg, had the eye-catching title "Are the Biological Differences Between Eskimos and North American Indians Truly Profound?" (Szathmary and Ossenberg 1978). This paper developed the position that Indians and Eskimos were not as distinct as many scholars had presumed (cf. Laughlin 1963, 1966), even suggesting that the two groups might have differentiated from a common stock after their arrival in the New World. Until this time, authors had disagreed on the number of possible migrations to the New World, but the consensus was that the ancestors of Aleut-Eskimos constituted not only a separate migration but the last major migration across the Bering Strait. While the arguments and analysis in these works are interesting, Szathmary limited her comparisons between Aleut-Eskimos and northern Indians of the American Subarctic, to wit Athapaskans in the west and Algonquians in the east. It is now well established that these northern groups are more similar to Eskimo-Aleuts than Indian groups from Mesoamerica, Central America, and South America (cf. Schanfield 1992; Cavalli-Sforza et al. 1994).

Authors who focus on GM allotypes have proposed different migration scenarios to account for variation in immunoglobulin genetic variants. Williams et al. (1985) observed that $Gm^{1;21}$ was present in "Paleo-Indians," Na-Dene, and Eskimo-Aleut samples, while $Gm^{1,2;21}$ was absent in Eskimo-Aleuts and $Gm^{1;11,13}$ was absent in Paleo-Indians. Na-Dene speakers had all three allotypes. This observation led the authors to conclude that Gm data supported the three-wave model of Greenberg et al. (1986) for peopling of the New World.

Also focusing on immunoglobulins, Schanfield (1992) pointed out that the work of both Szathmary (1993) and Williams et al. (1985) provided only a limited picture given their emphasis on North American native populations. When Schanfield synthesized Gm data from both North and South American populations, he found South Americans differed consistently from non-Na-Dene North American Indians, Na-Dene speakers, and Eskimo-Aleuts. He feels his data suggest that "in the peopling of the New World, at least four separate migrant groups crossed Beringia at various times" (Schanfield 1992, p. 381). He further suggested that the ancestors of South American Indians arrived before 17,000 BP while North American Indians arrived when the ice-free corridor opened up at the end of the Pleistocene. Both Eskimo-Aleuts and Na-Dene groups are thought to be later Holocene arrivals.

A grand synthesis of patterns of variation in nuclear genetic markers was accomplished by Cavalli-Sforza et al. (1994) in *The History and Geography of Human Genes*. This worldwide analysis of 120 markers in over 40 genetic systems devoted entire chapters to populations in each major geographic region, including a chapter on the Americas. To maximize the availability of genetic data across as many loci as possible, the authors combined data sets and came up with 23 New World groups, defined primarily on linguistic grounds. Importantly, the analysis included several Eskimo, Na-Dene, Siberian, North American, and South American groupings. After conducting a variety of distance analyses and two- and three-dimensional ordinations, Cavalli-Sforza et al. (1994, pp. 340–341) concluded:

> The genetic patterns in the Americas fully confirm the three waves of migration suggested by dental and linguistic evidence: Amerinds, Na-Dene, and Eskimo. Their order in time is strongly suggested by their north-south geographical order. Further refinements may reveal that more than one entry contributed to the first wave, but the archeological information is contradictory and our understanding of the genetic pattern of Amerinds is incomplete, so that further investigations are required to settle this problem.

Going well beyond classic nuclear markers, Reich et al. (2012) addressed the issue of origins through the analysis of 364,470 single-nucleotide polymorphisms in 52 Native American, 17 Siberian, and 57 "other" populations. They found evidence for three migration streams into the New World. The initial stream, which they call "First Americans," is comprised of American Indians from South America, Central America, Mesoamerica, and a few groups near the US-Mexican border. The second stream is "Eskimo-Aleut." Significantly, Greenland Eskimos and Aleuts cluster with Northeast Siberians, in line with earlier results on genetic markers and dental morphology. The third stream is represented by a single Chipewyan (Na-Dene) sample; this group also clusters with Algonquians of the eastern Subarctic, a point also made by Scott and Turner (2006). Reich et al. (2012, p. 373) suggest their results "are consistent with a three-wave model proposed mostly on the basis of dental morphology and a controversial interpretation of the linguistic data." Despite defining three distinct migration streams, they note that the second and third streams (i.e., Eskimo-Aleut, Na-Dene) are strongly admixed with First Americans. Despite this caveat, this meta-analysis supports what has long been contended on the basis of dental morphology; that is, Macro-Indians (or First Americans) from North, Central, and South America show homogeneity supporting a relatively recent common ancestor, with no evidence to suggest a second and separate ancestor for South American Indians. The analysis also revealed that Eskimo-Aleuts and Na-Dene-Algonquian represent two additional movements into the New World, a finding that is not totally obscured by later admixture with First American populations. Just as many are disparaging the three-wave model for the peopling of the Americas (cf. Stojanowski et al. 2013), Reich et al. (2012) step forward with evidence suggesting there is still life in the "dusty proposal" put forward by Greenberg et al. (1986) almost 30 years ago.

Mitochondrial DNA

When geneticists first discovered that mutationally induced variation in mitochondrial DNA (mtDNA) might help unravel human evolutionary history, there were severe sampling limitations. To harvest enough mtDNA for analysis, researchers had to collect human placentas, often a formidable task. The development of PCR (polymerase chain reaction) techniques in the early 1990s allowed researchers to obtain mtDNA samples from many kinds of tissue samples, including bone.

This development revolutionized the study of mtDNA, and research teams quickly pursued historical questions on every continent, among both living and earlier human populations.

Although mtDNA variation has been evaluated in groups throughout the world, the geographic region that has received an inordinate amount of attention is the New World. Because of sampling limitations, the early studies were regional in scope (Ward et al. 1991, 1993; Shields et al. 1992, 1993). With improved methods, expanding sample sizes, and cooperation among research teams, groups eventually addressed bigger issues regarding the internal differentiation of New World populations and dispersal dates from ancestral Asian populations (Wallace and Torroni 1992; Torroni et al. 1993, 1994; Forster et al. 1996; Malhi et al. 2002; Eshleman et al. 2003).

Mitochondrial DNA variation is studied through a combination of restriction fragment length polymorphisms (RFLPs) and direct nucleotide sequencing of the relatively short hypervariable control region (HVR-I and II). Haplogroups are distinguished by a combination of RFLPs and HVR-I and HVR-II polymorphisms (Schurr 2004a).

Jobling et al. (2004, p. 291) show the worldwide distribution of the major mtDNA clades, or haplogroups. Of the 27 major clades shown (lettered A to Z), New World populations exhibit the presence of only five haplogroups – A, B, C, D, and X. Numerous articles have been devoted to the issues of (1) how these haplogroups vary within and among Native American populations, (2) whether or not they were brought by separate founding groups or differentiated after arrival in the New World, and (3) the time depth for the origin of each haplogroup.

Regarding mtDNA haplogroup variation, North, Central, and South American Indians (Amerinds) all exhibit haplogroups A, B, C, and D. Eskimo-Aleuts, by contrast, have essentially no B and very little C (Schurr 2004a). Athapaskans were initially thought to lack the B haplogroup (Lorenz and Smith 1994), but it now appears to be present but infrequent in Na-Dene-speaking groups. Haplogroup X is limited to northern North American Indians from the Northwest Coast and Subarctic culture areas (Brown et al. 1998).

While the pattern of mtDNA haplogroup variation is coming into focus, opinions on the meaning of this variation have yet to reach a consensus. Some early studies favored the notion that the haplogroups indicated four separate migrations into the New World (Schurr et al. 1990; Horai et al. 1993; Lorenz and Smith 1996). Torroni et al. (1994) concluded there were three migrations: two Amerind migrations, with an early dispersal of A, C, and D, and a later migration that involved the B haplogroup. Athapaskans, with an exceptionally high frequency of the A haplogroups, were thought to constitute a third migration. Starikovskaya et al. (1998) also believed there was an early migration that carried the A, C, and D haplogroups with a later migration bringing B. Although there are several proponents of multiple migrations, the majority of researchers contend that the mitochondrial DNA variation evident among all Native Americans is best explained by a single migration event with haplogroup differentiation occurring after arrival in the Americas (Merriwether 1995, 2002; Kolman et al. 1996; Merriwether et al. 1996; Bonatto and Salzano 1997; Malhi et al. 2002; Silva et al. 2002).

From the outset, geneticists have argued that mtDNA is useful not only for describing patterns of variation but also for estimating times of divergence on a branching tree. Using either coalescence or distance methods of estimation in conjunction with several assumed mutation rates, most researchers addressing the issue of the initial New World settlement have arrived at very old dates for this event (Schurr 2004b). Several authors contend the first wave of migrants arrived in the Americas more than 30,000 years ago (Bonatto and Salzano 1997; Starikovskaya et al. 1998). Other workers give dispersal estimates of between 20000 and 30,000 BP (Torroni et al. 1994; Silva et al. 2002). Starikovskaya et al. (1998) dated early Amerinds at 34,000–26,000 BP with a later migration at 16,000–13,000 BP. Torroni et al. (1994) tried to come up with an estimate that agreed with either an early entry date (30,000+ BP) or a late entry date (ca. 13,000 BP) compatible with the Clovis-first model. Instead of coming down on one side or the other of this debate, their estimate fell in the middle with a range of 22,000–29,000 years ago.

Despite differing opinions on the numbers of migrations and times of dispersal, mtDNA geneticists are in fundamental agreement that Native American haplogroups are of Siberian origin. Torroni et al. (1994, p. 1162) reflect the sentiments of many when they say "We accept that all significant human entry into the Americas was by way of Siberia during periods of glaciation, when a land bridge connected Siberia and the extreme northwest of the Americas." When haplogroup X was discovered in American Indians, this was initially thought to represent a possible migration from Europe, or at least some founding Amerinds had Caucasian ancestry (Brown et al. 1998). If so, why is there no haplogroup H in Native Americans, as this is far more common in Europeans (ca. 40 %) than haplogroup X (ca. 2 %) (Schurr 2004a)? An alternative to a direct trans-Atlantic migration of X-bearing Europeans was developed by Reidla et al. (2003) who feel that haplogroup X represents a fifth rare mtDNA clade that came into the Americas across Eurasia, originating as far west as the Near East (Reidla et al. 2003). Finally, there are no haplogroups that link modern or ancient Americans to Southeast Asian or South Pacific populations, a population source for early Americans favored by some osteologists (Neves and Pucciarelli 1991; Steele and Powell 1992, 1997; Powell and Neves 1999).

Taking a somewhat unconventional approach, Perego et al. (2009) addressed the issue of migration routes into the Americas through the analysis of two rare mtDNA haplogroups: D4h3 and X2a. The distribution of D4h3 is primarily along the Pacific coast, with most samples coming from South America but also some from Mexico and California. With but one exception, this haplogroup is limited to the Americas but the exception is interesting. One individual from eastern China had the D4h3 haplogroup and control-region motif of 16301–16343 comparable to that in Native Americans. The senior author has long contended that China was a possible geographic source for Native Americans and this one small puzzle piece supports that position. The other haplogroup, X2a, is found exclusively in the Great Lakes region, Great Plains, and western Canada. It has been found only in the Americas. Perego et al. (2009) feel the divergence times for these two haplogroups was almost coincident at around 16,000 BP. Whether it happened before or after entry into the New World is not clear. The distribution of the two haplogroups suggests that the ancestral groups may have entered the New World along two different paths: D4h3 along the Pacific coast and X2a following an interior route (O'Rourke 2009).

A combination of archaeology and genetic variation has led researchers to develop a Beringian Standstill model (Tamm et al. 2007). Although sites in Alaska do not go back beyond the late Pleistocene, Pitulko and his colleagues (2013) have excavated the Yana Rhinoceros Horn site in northern Siberia that goes back 30,000 BP. The abundant material and zoological remains at this site show that people were well adapted to the rigors of an Arctic environment during the early Upper Paleolithic. In conjunction with genetic diversity that is unique to Native Americans, the Yana site raises the possibility that groups could have entered Beringia at least 30,000 BP but could not move further into the Americas because of major physiographic barriers (i.e., ice sheets, glaciers). During the standstill (also called Beringian incubation model), the Asian progenitors of Native Americans had ample temporal and spatial opportunity to differentiate within the broad confines of Beringia. When environmental conditions improved around 15,000 BP, populations could disperse south along a Pacific coastal route and/or via an interior corridor and carry their genetic differences with them.

Y Chromosome

As a complement to mtDNA, recent genetic studies that focus on the settlement of the Americas are evaluating recently discovered polymorphisms on the Y chromosome. The long neglected Y, whose strict paternal transmission complements the maternal transmission of mitochondrial DNA, exhibits two major types of polymorphisms on the nonrecombining segment (NRY) of the chromosome. First, there are point mutations that result in single-nucleotide polymorphisms (SNPs). The mutation rates for these polymorphisms are slower than for the second type of polymorphism – short tandem repeats (STRs). Taken together, researchers use SNPs and STRs to define a diverse array of haplogroups and haplotypes. As with mtDNA, Y chromosome polymorphisms have been used to estimate the number of migrations, the timing of dispersal of populations to the Americas, and the Old World sources for this peopling event.

Evolving and diverse nomenclatural systems applied to Y polymorphisms make the literature on this system difficult to decode for nonspecialists. To allay confusion, workers convened a consortium in 2001 to develop a common set of standardized terms for Y chromosome binary haplogroups (Y Chromosome Consortium 2002; Hammer and Zegura 2002). Based on this new system, it appears that most Native Americans exhibit haplogroup Q, an observation that led some workers to conclude that a single founding male lineage is sufficient to account for the ancestry of all Native Americans (Tarazona-Santos and Santos 2002; Jobling et al. 2004). Haplogroup Q is, however, defined on the basis of several distinct SNPs and

STRs, which other workers have interpreted as indications of multiple migrations from Asia. Lell et al. (2002) suggest that the Q-M3 and P-M45a Y haplogroups dispersed eastward from central Siberia along with the C and D haplogroups of mtDNA. Moreover, these authors feel that the haplogroups P-M45b and RSP4Y came from south Siberia along with a subgroup of the A haplogroup of mtDNA (control-region sequence variant 16192T and the *Rsa*I polymorphism at np16392). Karafet et al. (1999) and Ruiz-Linares et al. (1999) also conclude there were at least two founding Y haplogroups in the Americas.

Regarding the timing of dispersal, most estimates for arrival in the New World favor the long chronology (cf. Schurr 2004b). For their two migrations, Lell et al. (2002) estimate the first wave arrived in the New World ca. 20,000–30,000 BP with the second wave arriving much later, ca. 7,000–9,500 years ago. In contrast to those who see great time depth for Y haplogroups in the Americas, Seielstad et al. (2003) attempted to set an upper limit for initial entry into the New World based on a mutation (M242) that occurred just before the arrival of populations in the New World. Using a mutation rate of 0.18 % per generation, the authors estimated that M242 arose around 15,000 BP. These workers, who consider 18,000 an upper limit for New World settlement, thus favor an entry into the New World that followed, rather than preceded, the Last Glacial Maximum.

Macro-Indian Dental Variation

Now that contrasting models for the peopling of the New World from skeletal biology and genetics have been briefly reviewed, the case that can be made from tooth crown and root morphology will be presented in more detail. Table 1 lists the archaeologically derived Indian series used in this chapter. Altogether 3,584 individuals are represented in 17 North American groups and 11 South American groups. All the data in Table 1 were collected by the senior author. A key set of 29 largely independent, normal, age- and sex-free crown and root traits were scored for occurrence and expression using the Arizona State University dental anthropology system (Turner et al. 1991). An overwhelming number of individuals are pre-Columbian in age. Hence, there is little chance for European, African, or Oceanic admixture in this Pan-American assemblage, whose chronometric ages range from protohistoric to late Paleo-Indian. Although the exact modes of inheritance are still under investigation for these and other dental traits, it is believed that each has a substantial genetic component for occurrence and expression (Scott 1973; Harris 1977; Berry 1978; Scott and Turner 1988, 1997; Nichol 1990).

Space limitations permit reviewing only a few of the 29 traits, so mainly those that distinguish Northeast Asian Sinodonty from Southeast Asian Sundadonty are presented (Turner 1983, 1987, 1990a). Figures 1 and 2 illustrate five of these traits – incisor shoveling, double shoveling, *tuberculum dentale*, and first and second lower molar root number

Table 1 Frequency variation in archaeological New World dental samples[a]

	Shovel UI1		Uto-Aztec		Enamel ext. UM1		One-root UP1	
Trait, tooth break point	2–7/0–7		UP1 1/0–1		1–3/0–3		1/1–3	
Sample	%	No.	%	No.	%	No.	%	No.
North America								
Archaic Canada	86.9	38	0.0	34	12.9	84	78.7	80
Iroquois Canada	71.7	39	0.0	116	26.0	231	75.4	207
Maryland	93.7	48	0.0	54	35.8	106	81.9	94
Athapaskan	70.0	10	–	0	33.3	66	89.2	83
California	97.7	88	1.1	91	41.7	213	83.9	211
Grand Gulch, Utah	100.0	7	0.0	33	45.9	48	94.1	51
Chelly and Kayenta	97.6	42	1.7	59	61.4	96	97.4	76
Chavez Pass	71.4	7	4.2	24	55.1	29	83.9	31
New Mexico	87.5	120	0.8	128	45.9	170	91.5	141
Grasshopper	91.0	133	4.0	124	49.1	157	84.0	81
Pt. Pines early	87.5	24	2.6	38	58.8	51	85.0	40
Pt. Pines late	97.0	33	0.0	44	49.2	61	85.5	55
Arkansas	87.8	49	4.1	97	33.1	127	88.8	125
Alabama	97.3	146	1.9	159	34.0	203	77.8	108
Coahuila, Mex.	75.0	8	6.5	31	21.1	76	87.3	63
Cuicuilco and Tehuacan	94.7	38	1.7	59	33.3	66	91.2	57
Tlatelolco	100.0	39	0.0	85	50.8	122	91.0	122
No.		797/869		20/1176		743/1906		1386/1625
South America								
Panama	94.1	51	0.0	43	52.3	67	92.7	55
Ayalan, Ecuador	90.2	51	1.4	74	44.3	106	88.7	97
Cotocollao, Ec.	100.0	28	3.7	27	54.0	37	89.3	28

Chanduy, Ec.	88.2	17	0.0	12	40.0	20	94.7	19
Santa Elena, Ecuador	100.0	31	0.0	25	45.0	20	69.6	23
Paloma, Peru	86.5	52	0.0	29	46.2	78	88.1	101
Peru 1 and 2	90.0	50	0.0	118	48.4	310	86.7	450
Chile	92.2	64	0.0	65	71.7	127	96.9	128
Coronado, Brz.	95.0	20	0.0	34	36.0	61	90.5	42
Lagoa Sta, Brz.	91.4	35	1.8	56	33.3	78	83.6	73
Sambaqui, Brz.	91.1	68	0.0	74	55.5	146	84.7	111
No.		429/467		3/557		525/1050		992/1127
North America								
Mean	91.7		1.7		39.0		85.3	
Range	70.0–100.0		0.0–6.5		21.1–61.4		75.4–97.4	
South America								
Mean	91.9		0.5		50.0		88.0	
Range	86.5–100.0		0.0–3.7		33.3–71.7		69.6–96.9	
NA/SA Ï‡^{2} 1 d.f.P	0.0160.9		3.892		33.6		4.2	
			0.05–0.02		< 0.01		0.05–.02	

	Cusp 6		4-cusped		3-rooted		Y groove	
Trait, tooth break point	LM1 1–5/0–5		LM2 4/4–6		LM1 3/1–3		LM2 Y/Y+X	
Sample	%	No.	%	No.	%	No.	%	No.
North America								
Archaic Canada	65.2	69	8.3	84	10.5	124	5.3	76
Iroquois Canada	56.6	152	9.2	163	7.4	230	13.2	167
Maryland	41.8	91	8.8	102	6.0	150	11.5	96
Athapaskan	52.4	21	2.7	37	9.2	76	12.1	33
California	60.0	95	5.1	197	8.2	292	12.0	184
Grand Gulch, Utah	76.9	13	8.3	24	2.3	43	3.6	28

(*continued*)

Table 1 (continued)

Trait, tooth break point	Cusp 6 LM1 1–5/0–5		4-cusped LM2 4/4–6		3-rooted LM1 3/1–3		Y groove LM2 Y/Y+X	
Chelly and Kayenta	57.1	49	10.8	74	7.2	97	3.7	82
Chavez Pass	61.5	13	25.0	20	3.8	26	18.2	22
New Mexico	39.4	94	8.0	138	4.2	167	8.6	152
Grasshopper	47.3	148	17.3	104	5.9	135	17.6	119
Pt. Pines early	45.9	37	16.0	50	4.8	63	3.6	56
Pt. Pines late	43.6	39	13.0	54	12.3	65	8.8	57
Arkansas	55.7	79	8.5	118	5.3	150	12.4	121
Alabama	67.7	127	3.4	178	5.1	178	7.6	170
Coahuila, Mex.	61.5	26	7.9	38	5.4	56	12.8	39
Cuicuilco and Tehuacan	51.9	52	2.8	72	10.1	89	7.4	81
Tlatelolco	65.2	132	5.3	151	5.2	173	16.9	154
No.		683/1237		130/1604		143/2114		177/1637
South America								
Panama	61.9	63	11.4	70	5.6	90	1.4	72
Ayalan, Ecuador	66.2	68	7.8	77	3.7	108	3.8	79
Cotocollao, Ec.	52.2	23	12.5	40	8.8	34	7.9	38

Chanduy, Ec.	35.7	14	15.8	19	3.6	28	5.3	19
Santa Elena, Ecuador	80.0	10	5.7	35	4.7	43	3.3	30
Paloma, Peru	43.1	51	1.5	66	2.8	107	7.6	66
Peru 1 and 2	61.3	119	8.6	197	5.1	217	7.9	152
Chile	42.2	45	10.7	75	7.7	155	8.5	82
Coronado, Brz.	64.1	39	16.1	56	5.4	56	0.0	54
Lagoa Sta, Brz.	54.2	48	9.5	63	16.8	101	3.9	76
Sambaqui, Brz.	60.9	69	6.2	113	3.1	161	19.5	128
No.		316/549		72/811		66/1100		61/796
North America								
Mean	55.2		8.1		6.8		10.8	
Range	41.8–76.9		2.7–25.0		2.3–12.3		3.6–18.2	
South America								
Mean	57.5		8.9		6.0		7.6	
Range	43.1–80.0		1.5–16.1		2.8–16.8		0.0–19.5	
NA/SA Ï‡^{2} 1 d.f.P	0.85		0.42		0.697		6.02	
	0.5–0.3		0.7–0.5		0.5–0.3		0.02–0.01	

[a] Individual count, sexes pooled, all prehistoric except Athapaskan sample and some Iroquois. Sample provenience and break points are detailed in Turner (1985) and elsewhere. Scoring is done with ASUDAS (Turner et al. 1991)

Fig. 1 *Arrow 1* indicates right upper central incisor shoveling trait in a female skull from prehistoric Alabama site Lu25–425. *Arrow 2* points to double shoveling. Not discussed in this report, but one of the key traits used in the multivariate analysis, *arrow 3* points to canine *tuberculum dentale* (CGT neg. no. 6-6-80:19)

Fig. 2 *Arrow 1* indicates left lower first molar with two roots in prehistoric Peruvian male from a cemetery in the Chicama Valley. Had there been a supernumerary third root, it would be out of view on the distolingual aspect. Not discussed in this report, but one of the key traits, *arrow 2* points to a one-rooted lower second molar (CGT neg. no.7-3-80:7. Reprinted courtesy of Dental Anthropology Newsletter)

Findings

American Indian dental morphological variation, assessed against the background of archaeological and linguistic information, led to the following generalizations:

1. There are three dental clusters of Macro-Indians: North America, South America, and an interregionally convergent group.
2. Dental variation is relatively low among Macro-Indians.
3. The Macro-Indian dental divisions arose by local evolution.
4. South America was colonized soon after North America.
5. Individual dental trait frequencies show only random variation.
6. Only Northeast Asian Sinodonty is present in the New World.
7. Dental variation supports the Clovis/epi-Clovis prehistory and Greenberg language migration models.

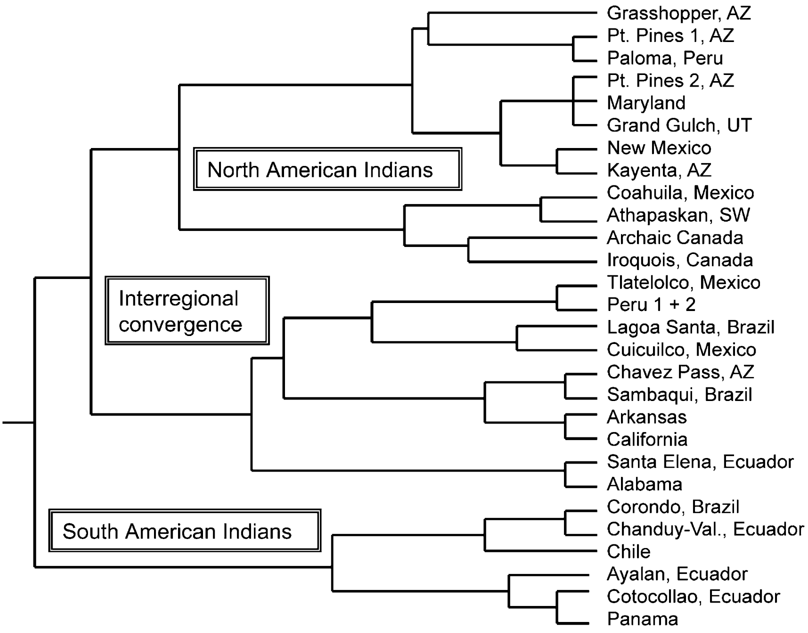

Fig. 3 Dendrogram of North and South American pre-Columbian dental relationships based on mean measures of divergence clustered with Ward's method, 29 dental traits. Computer reference: North and South America

Three dental clusters: Figure 3 is a dendrogram computed with Ward's clustering method for the 106 possible pairwise mean measures of divergence, a multivariate similarity/dissimilarity statistic developed by C.A.B. Smith (Berry and Berry 1967) with widely used adjustments for sample size and determination of statistical significance (references in Turner 1985). There are three primary dental groups: North America (at the top), South America (at the bottom), and a middle group that shows interregional convergence.

The Paloma sample is surely a misclassification attributable to chance. Some interregional convergence is expected given that dental microevolution (in the sense of gene frequency changes) is probably best explained as caused largely because of random changes due to founder's effect, population structure, and local genetic drift. There is no archaeological or other evidence to believe, for example, that the Ecuadorian Santa Elena series is similar to the Alabama sample because of ancestry closer than to each sample's respective regional relationships. Instead, the Santa Elena-Alabama similarity is most likely an example of the occasional convergences that should be expected if Macro-Indian dental evolution was mainly due to chance, not selection or gene flow. As will be discussed below, the relatively low amount of variation, despite the two main North and South American clusters, is not supportive of multiple Paleo-Indian migrations.

Low dental variation: Inspection of Table 1 reveals a low amount of trait frequency variation between the 29 groups relative to that in, say, eastern Asia or even New World Arctic people (Turner 1991). This limited New World Indian dental divergence is probably what causes the rather limited "treeness" of the dendrogram in Fig. 3. This suggests either substantial gene flow throughout the Americas or a relatively recent colonization of the Americas with only minor in situ dental differentiation. Excellent "treeness" has been obtained throughout the New World (Arctic, Subarctic, non-Arctic) with these same dental traits and statistical methods (Turner 1987). Table 1 shows that upper central incisor shoveling and lower first molar root number have very different overall frequencies in the New World. The former is a high frequency trait, and the latter, a low frequency trait. Scott (1973) demonstrated that trait frequency was positively correlated with trait expression in the offspring of specific mating types, providing strong evidence for polygenic inheritance. As can be seen, shoveling is universally high (>70 %) among the groups, whereas three-rooted lower first molars are uniformly at a low frequency, averaging about 6 %. Both traits have little variation within and between North and South America. These two traits, like the other 27, show no sign of clinal variation from north to south, east to west, coastal to interior, or low to high elevation. Trait frequencies have no identifiable gross environmental correlates in the New or Old World that would suggest the effects of short-term natural selection.

Dental divisions arose by local evolution: Table 1 also lists the North and South American means and ranges for eight traits, seven of which distinguish Sinodonty from Sundadonty, plus a trait found almost exclusively in Native Americans – the Uto-Aztecan premolar. The tabulation shows that there are no statistically significant differences in some traits and very little in all others except the enamel extension, between pre-Columbian North and South American Indians. None of these traits has a north-south mean difference greater than 6 % (enamel extensions). There is no tendency to exhibit less "Mongolization" or Sinodonty in South America than in North America, that is, there is no evidence for Sundadonty. The differences between the means appear to be mainly random. What little difference there is between North and South America is better interpreted as due to postcolonization local evolution rather than to pre-differentiated multiple migrations. Moreover, the archaeology, craniology, and odontology the senior author has personally seen and read about in Russian sources for eastern Siberia do not provide any cultural or biological basis for hypothesizing markedly differentiated source populations in Primorye, Chukotka, trans-Baikalia, or Yakutia. However, the fact that these Siberian geographic districts and their pre-Russian cultures are recognizable today and prehistorically could mean that they were also distinctive even earlier in Late Pleistocene times as well and would have served as incubator habitats for some amount of pre-Beringian biocultural and linguistic differentiation.

No genetic bottlenecking at Panama: Because there are few dental differences between North and South American Indians relative to even smaller area of eastern Asia, it would appear that there was no meaningful Paleo-Indian genetic bottlenecking in Panama. The size of the Paleo-Indian population wave that advanced through the isthmus was large enough to contain a representative sample of the North American Indian dental gene pool. A trait-by-trait comparison of presumed North and South American Paleo-Indians (Turner 1992a) turns up no differences greater than the within-continent range of trait occurrence. However, as is well known from various studies of blood group and DNA markers (Spuhler 1979; Szathmary 1979; Shields et al. 1992), the initial Paleo-Indian gene pool probably did not contain a representative sample of Chukotka genes, let alone Pan-Northeast Asian genes. For example, allele B of the ABO system was seemingly not carried across the Bering land bridge by Paleo-Indian colonists, and the three-rooted lower first molar gene(s) was carried by only a small proportion of the first Beringian migrants.

South America colonized soon after North America: In 1976, MacNeish suggested that North America was populated for some 100,000 years, while South America had been inhabited for only 25,000 years. Had this been the actual occupational history of the New World and if continuous occupation and regular postcolonization dental microevolution are assumed (Turner 1986), then the North American samples should have exhibited in Fig. 3, on the basis of time alone, about fourfold more internal dental divergence than do the samples from South America. That is, the secondary branching in North America should be much further to the left compared with South America. The dendrogram provides no support for unequal evolutionary time in North and South America, nor do the individual trait values in Table 1. Admittedly, variation in the rate of dental microevolution, connected as it must be to population structure, size, and demography, does not allow precise estimates of separation between branching populations, in this case North and South America. However, claims for 25,000–30,000 years of South American occupation are certainly pushing the envelope of credibility on the basis of both New World and Old World dental evolutionary considerations and most archaeological evidence (Lynch 1991; Haynes 2002a; Fiedel 2004). In the Old World, it is a question of the antiquity of Sinodonty, which may date to around the age for Upper Cave Zhoukoudian, sometime between 11,000 and 30,000 years BP (Chen et al. 1992).

Individual dental trait frequencies show only random variation: Comparisons of the means for North and South American dental trait frequencies (Table 1) show no identifiable trends that could be attributed to multiple migrations, differential geographic selection, or some other type of localized natural selection directly affecting teeth. While these samples are not ideal for rigorously assessing the likelihood of selection pressure, the more obvious correlates are absent. Hence, the dental samples of the South American Pacific coastal populations of Chanduy-Valdivia, Santa Elena, Paloma, Peru, and Chile are not especially similar according to the analysis in Fig. 3. These groups might be relatively similar due to some form of coastal environmental selection, but if this were so, then they should have also incorporated the coastal Sambaqui of Brazil. Samples from upland environments are not any better correlated than the coastal groups. Mountain-plateau-originating Grasshopper and Point of Pines 1 are linked to coastal Peru. Mountain-located Cotocollao clusters with coastal-lowland Panama. High rainfall and tropical coast Sambaqui folk are linked to low rainfall Arizona plateau Chavez Pass. The two long-lasting deep-winter Archaic Canada and Iroquois samples are joined, but their link with Coahuila from the cool winter high desert of northern Mexico does not suggest cold selection. Only city-state organization versus non-city-state seems to be a source of possible selection. Thus, Tlatelolco, a late and large central Mexican Aztec metropolis, clusters with the similarly developed Peruvian samples. Their clustering together may be the result of oral and other disease selection associated with agricultural economies and highly processed cereal and tuber foods. However, if caries selection had been responsible, then city-state-level Tlatelolco and Peru should have higher frequencies of simpler and potentially more caries-resistant teeth, such as 4-cusped lower second molars, less shoveling, and fewer first molar cusps 6, which is not the case for either sample. Still, disease selection requires further study with respect to dental morphology because caries are rare in hunters and gatherers but are very common among agriculturalists.

Only Sinodonty is present in the New World.

Shoveling: Figure 4 illustrates upper central incisor shoveling. Tables 1 and 2 show crown and root trait frequencies within the Americas, eastern Asia, Melanesia, Australia, and western Europe. Shoveling is very common throughout the Americas and in Northeast Asia. There is no significant difference in the shoveling frequencies of North America (91.7 %) and South America (91.9 %). It is less common in Southeast Asia and Australia, much less so in Melanesia, and very rare in western Europe. This trait alone shows that Paleo-Indians more likely originated in the north China-Mongolia gene pool than in those of the other areas. That gene pool, in turn, had to have had its morphogenetic origin in the Sundadont dental pattern of Southeast Asia and South China – the closest dental pattern in the world

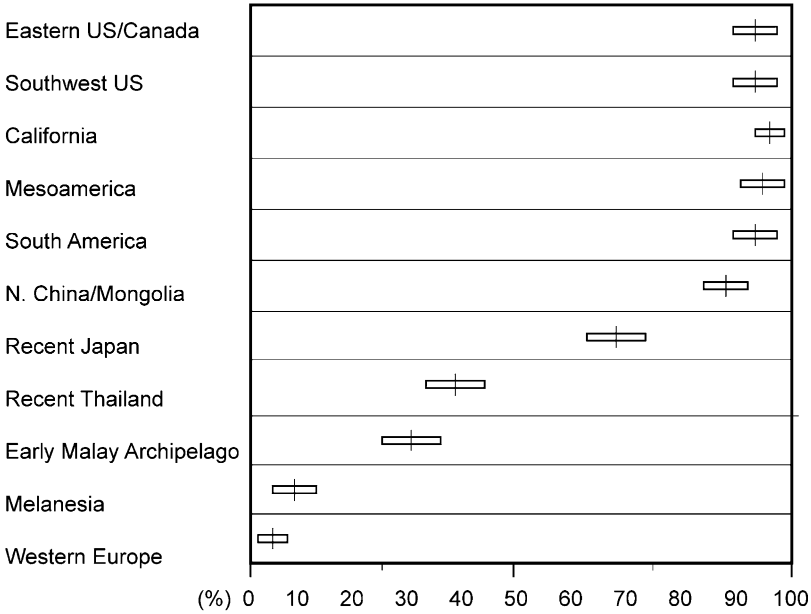

Fig. 4 Circum-Pacific and European frequencies of upper central incisor shoveling

Table 2 World dental frequency variation for the eight distinguishing Sinodont and Sundadont morphological traits[a]

Trait tooth break point	Shovel UI1 2–7/0–7	Double-shovel UI1 2–6/0–6	1-root UP1 1/1–3	Enamel extension UM1 1–3/0–3
Arctic[b]	78	75	95	46
Eastern USA and Canada	91	78	80	31
SW USA	91	65	89	51
California	98	90	84	42
Mesoamerica	94	93	89	39
South America	92	90	87	49
North China-Mongolia	84	30	77	51
Recent Japan	66	20	75	55
Recent Thailand	37	9	66	39
Early Malay Archipelago	30	28	68	18
Melanesia	9	5	57	4
Australia	20	1	58	9
West Europe	2	4	58	2

Trait tooth break point	Peg-reduced-C.A. UM3 prc/norm +prc	Deflecting wrinkle LM1 1–3/0–3	3-root LM1 3/1–3	1-root LM2 1/1–3
Arctic[b]	20	30	30	31
Eastern USA and Canada	18	45	6	32
SW USA	21	35	6	29
California	17	45	6	32
Mesoamerica	19	28	6	29
South America	25	38	6	37
North China-Mongolia	53	29	34	42
Recent Japan	42	35	24	33
Recent Thailand	18	19	11	31
Early Malay Archipelago	0	11	6	33
Melanesia	13	18	3	5
Australia	5	23	5	6
West Europe	12	7	1	27

U denotes upper, *L* lower, *CA* congenital absence

[a] Individual count, sexes pooled, historic and prehistoric native groups, sample provenience, and break points detailed in Turner (1985) and elsewhere

[b] Unpublished new grouping contains Aleut, Eskimo, Greenland Eskimo, Alaska Peninsula, Bering Sea, Kachemak, and Kodiak (computer file name: Arctic94)

to Sinodonty. Clearly, Paleo-Indians did not originate in Europe, Oceania, or Southeast Asia according to the distribution of the incisor shoveling genes. The African dental pattern is too different from that of Sinodonty to be considered relevant to Native American origins considerations (Turner 1992b).

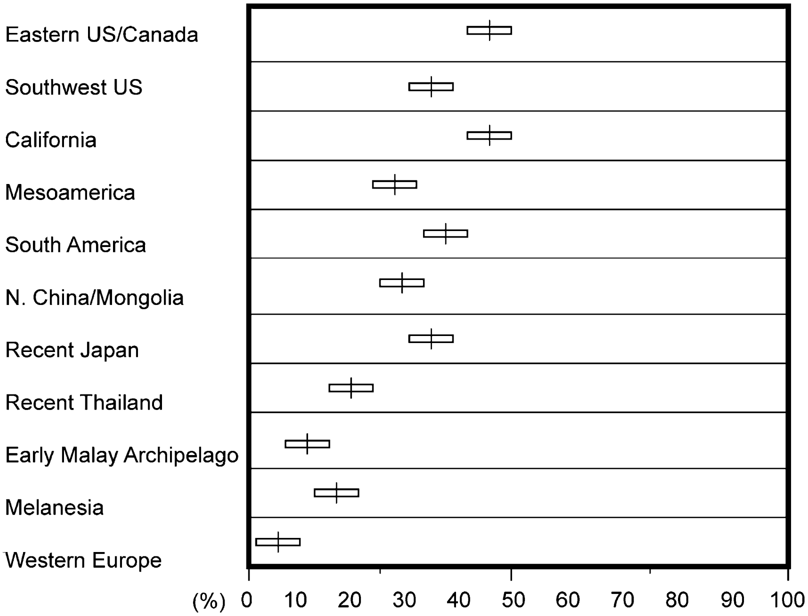

Fig. 5 Circum-Pacific and European frequencies of upper first molar enamel extension

The frequency of shoveling in the earliest North and South American crania is high (ca. 90.1 %) (Turner 1992a, p. 18), nearly identical to that of recent populations (Table 1). This apparent similarity is not what would be expected for the implication that the Kennewick skeleton was not a Sinodont (Powell and Rose 1999), as well as the claim that early South American skeletons were also not Sinodonts (Lahr 1995, p. 163).

Enamel extensions: Figure 5 shows the frequencies for the enamel extension polymorphism, a quasi-continuous trait found on the buccal surface of the upper first permanent molar. While shoveling might conceivably have some minor adaptive value (Mizoguchi 1985), it is difficult to imagine how selection could favor the tiny extension of enamel on the subgingival root surface. In fact, these smooth enamel extensions could have a slightly negative value because they do not provide a porous surface for periodontal tissue attachment, hence favoring the formation of periodontal disease pockets in the adjacent alveolar bone. Enamel extension variation provides essentially the same frequency picture as shoveling; namely, extensions are common in Indians and Northeast Asian Sinodonts, slightly less so in Southeast Asian Sundadonts and very uncommon in Melanesians, Australians, and Europeans.

One-rooted upper first premolar: Figure 6 shows the frequencies for the upper first (P3 in paleontological notation) premolar root number polymorphism, which can have one to three roots. As with the shoveling and enamel extensions, one-rooted upper first premolars are common in Northeast Asian Sinodonts and

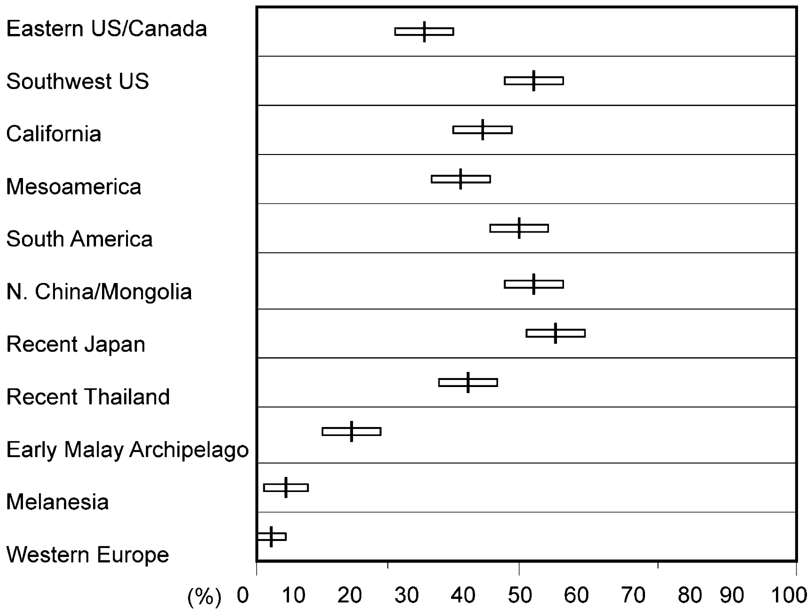

Fig. 6 Circum-Pacific and European frequencies of one-rooted upper first premolars (P3)

all pre-Columbian Indians, less common in Southeast Asian Sundadonts, and slightly less common in Melanesians, Australians, and western Europeans. While there is less continental Old World and South Pacific Islander occurrence of one-rooted upper first premolars, there is nothing in the data to suggest that American Indian ancestry was anything other than from Northeast Asian Sinodonts.

Deflecting wrinkle: Figure 7 shows the frequencies of another tiny secondary trait, the first permanent molar deflecting wrinkle. This polymorphism is the degree of distalward deflection from none to pronounced of the medial ridge of cusp 2 (mesiolingual cusp). This feature has almost no potential for adaptation as it is usually worn off the first molar by the beginning of reproductive age. The deflecting wrinkle is common in pre-Columbian American Indians and Northeast Asian Sinodonts. It is less frequent in Sundadonts and western Europeans. Melanesians and Australians are highly variable for the deflecting wrinkle, and the present Oceanic samples have a substantial frequency, fitting the geographic expectation of an old Southeast Asian origin for the ancestors of Pacific Islanders.

Three-rooted lower first molar: Figure 8 shows the frequencies for the three-rooted lower first permanent molar, another root polymorphism with one to three possible roots. Lower molar and upper premolar root numbers are statistically unrelated morphogenetic features. By far, worldwide, the two-rooted condition is most common for the lower first molar root number. The oldest known example of a three-rooted lower first molar in anatomically modern humans is the 22,000-year-old mandible fragment from the Tabon Caves site on Palawan Island in the western Philippines, excavated by Fox (1970). The fragment has three root sockets at the

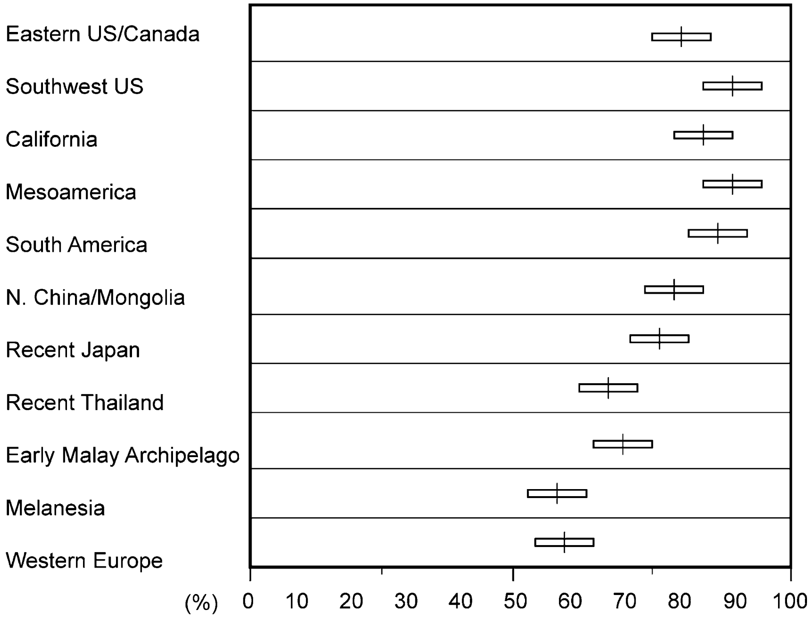

Fig. 7 Circum-Pacific and European frequencies of lower first molar deflecting wrinkle

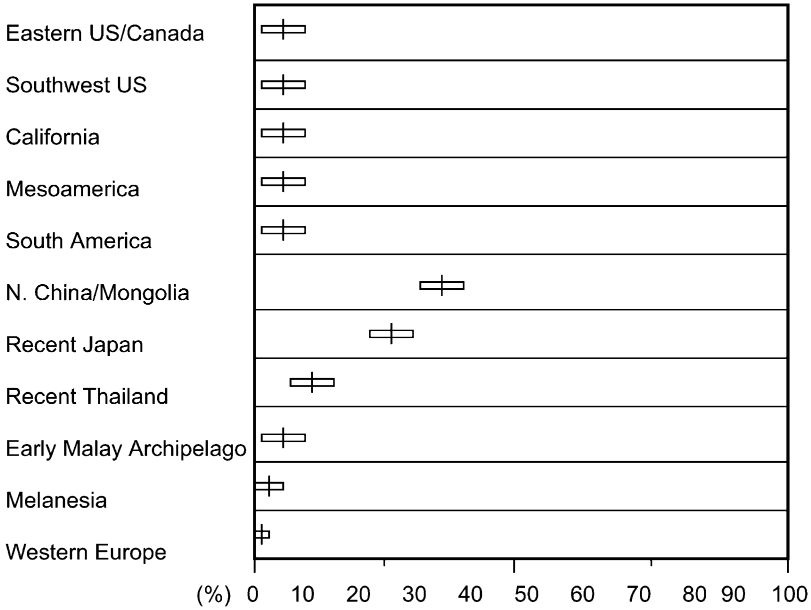

Fig. 8 Circum-Pacific and European frequencies of three-rooted lower first molars

first molar location. Three-rooted lower first molars are a Sinodont characteristic, but, like the missing B allele in living American Indians, Paleo-Indian colonists almost failed to carry to the New World the gene(s) responsible for this accessory root on the lower first molars.

Dentition Supports Ice-Free Corridor, Epi-Clovis/Clovis-First, and Macro-Indian Models

Unlike the other dental traits discussed here, three-rooted lower first molar frequency is less than that of Northeast Asian Sinodonts, and this trait is generally uncommon although uniformly present at about 5 % in pre-Columbian Indians. These characteristics imply two events. First, the initial number of Siberians to reach eastern Beringia was apparently small and not strongly representative for all genetic characters. Second, the trait's Pan-American uniformity suggests (1) that after crossing the ecologically patchy Bering land bridge, group size increased significantly because similar dental gene samples were carried southward to all other parts of the New World and (2) all American Indians discussed here are descended from the founding Siberian epi-Clovis migrants whose archaeological record for colonizing Alaska and Chukotka begins about 12,000 BP (Goebel et al. 2003). The demographic events of rapid population growth and widespread territorial expansion, leading to genetic stabilization in North and South America, could have occurred first in interior Alaska or later after subsequent generations reached and passed through the inhospitable and limiting corridor between the Cordilleran and Laurentide ice sheets of Canada. Unfortunately, there is nothing that can be identified in the dental data that help explain where and how the rapid expansion began, regardless of how one defines migration (i.e., wavelike, pulsed, clonal spread, chaotic drift, niche based, continuous leakage, leapfrogging, etc.), or which migration route one chooses ("ice-free corridor," Pacific coast, ice-crossings and polar desert trek to Atlantic coast, or some combination of these). However, given the rarity of Paleo-Indian sites in Alaska, the recent Fairbanks and Brooks Range finds notwithstanding (West 1981, 1996; Powers et al. 1990; Hoffecker et al. 1993; Kunz and Reanier 1994; Yesner 2001; Yesner and Pearson 2002, others), the model favored here is that of demographic growth, related faunal extinctions (Martin 1990), and genetic drift stabilization as having explosively started at the southern exit of the western Canadian ice sheet corridor. The corridor entry is favored over the coastal route because of the severe boating difficulty of getting past the Late Pleistocene glacial ice mass on and around the Alaska Peninsula (Elias 2002; Turner 2002; Hoffecker and Elias 2003). In contrast to the rarity of Clovis or Clovis-like fluted points along the entire Pacific coast of North America, Carlson (1991) identified at least 40 archaeological sites in the ice-free corridor area of British Columbia and Alberta that had various types of fluted points.

Elsewhere the senior author (Turner 1992a) inventoried a number of dental observations from crania that were "candidates" for Paleo-Indian chronometric status. None of these incomplete individuals deviated from the Sinodont pattern. Since then, he has examined the teeth of four other crania that are dated as Paleo-Indian or Early Archaic. These include Sulphur Springs woman, excavated in southern Arizona by Waters (1986), Horn Rock Shelter double burial near Waco, Texas, and the Wilson-Leonard female, also from Texas (Young et al. 1987; Steele 1989; Steele and Powell 1992). These four also conform to the Sinodont dental pattern as best as can be determined given the considerable amount of tooth wear they and other hunter-gatherers exhibit worldwide.

Finally, some archaeologists (reviewed in Dixon 1999; for opposition, see Carlson 1991; Haynes 2002b) and geneticists (discussed previously) have argued for a Pacific coastal entry route to North and South America from Siberia despite the absence of archaeological evidence for, and Alaska Peninsula glacial evidence against, such a route (Workman 2001; Turner 2003). Moreover, Macro-Indian language family distributions in the Americas, Penutian, for example (Ruhlen 2000), do not suggest Pacific coastal entry. As for dental morphology, the Pacific coast samples presented in Table 1 show no sign of meaningful differences with interior samples as would be expected, had there been an earlier more Sundadont-like migration or a fourth American variant of Sinodonty.

Conclusion

In assaying the different types of biological data brought to bear on the peopling of the Americas, there are disagreements on the numbers of migrations and their timing, but there are many points of agreement as well. The homogeneity among American Indians indicated by dental morphology is paralleled by mtDNA and Y chromosome haplogroup data and single-nucleotide polymorphism (SNP) arrays. The dentition shows a dichotomy between North American and South American Indians, and this is also evident in genetic markers. Several studies critique the three migration model of Greenberg et al. (1986), but these often fail to include data on Eskimo-Aleut populations. If researchers argue that mtDNA and Y chromosome data support a position that Eskimo-Aleuts differentiated from American Indians after the arrival of a common ancestor in the New World, there are serious problems with their data sets (or the interpretation thereof). On the basis of teeth, nuclear markers, and even craniometry, Eskimo-Aleuts are consistently more closely aligned with recent Asian populations than are American Indians.

The placement of other northern groups, especially Na-Dene speakers, is a bit less certain than the Eskimo-Aleut case. Based on similarities in mtDNA, Shields et al. (1993) concluded that Eskimo-Aleuts and Athapaskans were very closely related, diverging from one another in the American Arctic as recently as 7,000 years ago. This same general position has long been advocated by Szathmary (1979, 1981, 1993); Szathmary and Ossenberg 1978) based on the variation in blood group and serum protein polymorphisms. Cavalli-Sforza et al. (1994) found Na-Dene groups fell between Eskimo-Aleuts and Amerinds in general. This intermediary position is also indicated by dental morphological variation (Turner 1985; Scott 1991;

Scott and Turner 1997, 2008). When ancillary fields are taken into account, especially linguistics and archaeology, it is hard to reconcile common origins for Eskimo-Aleuts and Na-Dene speakers in the Holocene. Even rare genetic markers speak against this purported tie. Albumin Algonquin (formerly Albumin Naskapi) is found in polymorphic frequencies in Athapaskans and Algonquians but not in Eskimos (Lampl and Blumberg 1979). Eskimos have the B allele and Subarctic Indians do not (Harper 1980). The Y chromosome haplogroup C-M130 has also been found exclusively in Athapaskan and Algonquian populations (Schurr 2004a).

The level of genetic diversity in the Americas has led some authors to conclude that the New World was peopled long before the Last Glacial Maximum, with many estimates exceeding 30,000 years BP. To a considerable extent, this runs counter to what is known about the archaeology of Siberia and Beringia, let alone Australia whose aborigines' biology, tools, and language have evolved so much that few resemblances remain with their Southeast Asian homeland. The New World founding population had to have been in place in Northeast Asia before any groups could start budding off to colonize the Beringian landscape. In a recent synthesis of mtDNA and Y chromosome analyses, Schurr (2004a) proposes three major peopling events from Asia to the Americas: (1) the initial founding population in the Americas came from south-central Siberia and arrived in the New World between 20,000 and 14,000 cal year BP; given the presence of ice sheets across the breadth of Canada, the route of this migration is presumed to be coastal; (2) a second migration, following an interior route, contributed to many of the populations of North and Central America; and (3) Beringian populations, including the ancestors of Aleuts, Eskimos, and Na-Dene speakers, came into New World following the Last Glacial Maximum.

Although Schurr's reconstruction parallels dental findings in a number of ways, the degree of dental differentiation in the New World still favors a late entry model, a position more in line with current archaeological knowledge (Haynes 2002a; Fiedel 2004) and some genetic studies (cf. Seielstad et al. 2003). In principle, there is no objection to an earlier date for the peopling of the New World. At present, a compelling case has not been made for this position, especially in light of archaeological success in Australia in finding very early sites by a much smaller number of archaeologists and geologists (Jelinek 1992). If a coastal migration did take place, more evidence for this event is required. For example, of all the pre-Clovis archaeological sites listed by Schurr (2004a) to support early entry, none are along the Pacific coast. Scholars will continue to find "pre-Clovis" sites and develop molecular clocks and models of linguistic differentiation that indicate early human entry into the Americas, but the final arbiter of dispersal will come from archaeological sites that have excellent stratigraphy and no dating issues. Granted, a major problem associated with a coastal migration is the presumption that most early sites are now under water and mostly inaccessible.

The dental characteristics of pre-Columbian American Indians easily fit with both the hypothesis of a rapidly expanding Clovis- or epi-Clovis first colonization event, long advocated by Martin (1990) and Haynes (1991), and the Macro-Indian language evolution model developed by Greenberg (1990). Because all prehistoric and unadmixed living Native Americans, including Na-Dene/Greater Northwest Coast and Aleut-Eskimo, only briefly discussed here, have the Sinodont dental pattern, it would seem that when a date for the emergence of full-blown Sinodonty in Asia is established with some certainty, then that will have to be the earliest possible date for the subsequent colonization of the Americas, assuming that early and late similarity actually means genetic continuity. Inasmuch as the Upper Cave crania seem to have a Sinodont dental pattern, then whatever date is finally settled on for that assemblage will provide a reasonable time estimate for the potential colonization of the Americas.

It is necessary to focus on Upper Cave since there are only a few sites in Siberia with Late Pleistocene human remains. One site near Lake Baikal, called Mal'ta, seems to have European- rather than Asian-like teeth (Turner 1990b), an observation supported by aDNA which shows individuals from this site had the European haplogroup U (Willerslev 2013). Two sites west of Lake Baikal have physical anthropological signs of "Mongoloid" or Sinodonty. These are the Late Pleistocene Yenisei River sites in and near Krasnoyarsk. In the city of Afontova Gora, a fragment of a subadult frontal bone found in a river bank section was thought to have been Mongoloid because of the size and form of the adhering nasal bones (Alekseev 1998). Upstream ca. 35 km (21 mi) is Listvenka, from which came a mandible of a child whose unerupted first molar is slightly more Asian than European in overall appearance. Hence, broadly speaking, the pre-Arctic ancestral homeland of Paleo-Indians must have been in north China, Mongolia, and southern Siberia. It is easy to envision how newly evolved Sinodonts quickly expanded into northeastern Siberia, after they succeeded in domesticating the dog for hunting and hauling, perhaps drifting north out of China via the Vitim River system. Although people were in northern Siberia at 30,000 BP (Pitulko et al. 2013), population density above the Arctic Circle was likely circumscribed so the ancestral Paleo-Indian northward drift would have been rapid and with little human resistance in Beringia. Because the dental differences between the north China-Mongolia group and all unadmixed Indians are small compared with the much larger difference between Northeast and Southeast Asians, the relatively small amount of intra-trait dental variation within the New World may reflect the simple evolutionary fact that Sinodonts have been in the Americas for a relatively short period of time, less time than it took for Sinodonty to evolve out of Sundadonty. Moreover, the colonists and their dogs were so reproductively successful that the usual genetic drift cause of short-term dental trait frequency change was reduced or negated by the large population size that quickly grew south of the east Beringian Arctic steppe. This evolutionary scenario, despite years of bioarchaeological research, does not differ much from that first proposed on craniological grounds by Hrdlička (1925). While some readers may find such lack of theoretical and empirical change as unthinkable in the rapidly changing world of science, others, ourselves included, recognize it as a tribute to Hrdlička's empirical orientation and one of the more probable scenarios in the complex world history of Late Pleistocene human microevolution and dispersal. For the present, Macro-Indian dental variation is not supportive of a Pacific coastal entry route to North and South America, leaving the late entry ice-free corridor model as dentally most parsimonious.

Cross-References

- ▶ Ancient DNA
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ General Principles of Evolutionary Morphology
- ▶ Overview of Paleolithic Archaeology
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Population Biology and Population Genetics of Pleistocene Hominins
- ▶ Species Concepts and Speciation: Facts and Fantasies

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Overview of Paleolithic Archaeology

Nicholas Toth and Kathy Schick

Contents

Abstract

The Paleolithic, or Old Stone Age, comprises over 99 % of human technological history and spans a time range from 2.6 Ma (the earliest recognizable stone tools and archaeological record) to 10,000 years ago (the end of the last ice age). There are three major stages of the Paleolithic: (1) The Early Paleolithic which includes the following: (a) the Oldowan, from 2.6 to about 1.0 Ma, characterized by simple core forms on cobbles and chunks (choppers, discoids, polyhedrons), battered percussors (hammerstones and spheroids), flakes and fragments, and retouched forms such as flake scrapers. Cut marks and fracture patterns on animal bones indicate meat and marrow processing, with the use of simple stone knives and hammers. This stage is associated with the later australopithecines and the earliest forms of the larger-brained genus *Homo* and documents the first hominid dispersal out of Africa and into Eurasia, (b) The Acheulean, which lasted from approximately 1.7 Ma to 250,000 years ago and was

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N. Toth (✉) • K. Schick
Stone Age Institute and Indiana University, Bloomington, IN, USA
e-mail: toth@indiana.edu; kaschick@indiana.edu

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characterized by large bifaces such as handaxes, cleavers, and picks. The early Acheulean is associated with *Homo erectus/ergaster*, while the later Acheulean (by ca. 500,000 years ago) is associated with the even larger-brained *Homo heidelbergensis*. (2) The Middle Paleolithic/Middle Stone Age, from about 250,000 to 30,000 years ago, characterized by a focus on retouched flake tools, such as scrapers, points, and backed knives, and prepared core technologies such as the Levallois method. The controlled production and use of fire appears to be widespread for the first time. This stage is especially associated with archaic forms of *Homo sapiens* (having modern-size brains but more robust faces and postcranial skeletons), including the Neanderthals (see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3) and the earliest anatomically modern humans (see chapter "▶ Origin of Modern Humans," Vol. 3). (3) The Late Paleolithic, from 40,000 until 10,000 years ago, characterized by blade tool industries; a proliferation of artifacts in bone, antler, and ivory; and the emergence of rich symbolic art in the form of paintings, engravings, sculpture, and personal body adornment (see chapters "▶ Modeling the Past: Archaeology," Vol. 1, "▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia," and "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3). Early examples of clear architectural structures, musical instruments, and mechanical devices (spear-throwers and bows and arrows) appear during this time. This stage is especially associated with anatomically modern humans, *Homo sapiens sapiens*.

Introduction

The Paleolithic is the term applied to a very broad, early period of human prehistory beginning with the first archaeological evidence of stone toolmaking approximately 2.6 Ma, through to the end of the Pleistocene epoch about 10,000 years ago, when the last continental glaciation receded. It documents the emergence of a wide range of new technological, behavioral, and adaptive traits through time (Toth and Schick 2010). It is important to appreciate that over 99 % of human technological development took place during the Paleolithic. The Paleolithic thus constitutes the bulk of the time span of human technological development and human prehistory and documents the emergence and evolution of the genus *Homo*. The term is applied primarily to prehistoric developments in the Old World, as the New World's earliest archaeological evidence appears only toward the very end of Paleolithic times, during the last phases of the terminal Pleistocene glaciation. In the New World, however, the period of Late Ice Age hunter-gatherers is often referred to as "Paleo-Indian" and is contemporaneous with the last few thousand years of the Paleolithic in the Old World. For overviews of human evolution and the Paleolithic, see also Boyd and Silk (2012), Burenhult (2003), Clark (1982), Ciochon and Fleagle (2006), Delson et al. (2000), Gamble (1986), Johanson and Edgar (1996), Jones et al. (1992), Klein (2009), Lewin and Foley (2004), Mithen (1996), Noble and Davidson (1996), Renfrew and Bahn (1996), Roberts (2011), Scarre (2013), Schick and Toth (1993), Stringer and Andrews (2005), Tattersall (1999), Tattersall and Schwartz (2000), and Toth and Schick (2010).

"Paleolithic" literally means the "Old Stone" (paleo = old, lithic = stone) Age, as it represents the earliest phases of human technological development when the vast majority of the tools represented in the archaeological record were made of stone. At the end of the Pleistocene, the Paleolithic is followed by the later phases of the Stone Age, the Mesolithic and then the Neolithic. During the Mesolithic (in some regions referred to as the "Epipaleolithic"), stone technologies continued to evolve as stone tool-using hunter-gatherers adapted to changing environments of the current (Holocene) epoch, sometimes characterized by small (microlithic) stone tools. During the last phase of the Stone Age, often referred to as the Neolithic (or "New Stone" Age), a transition occurred from hunting-gathering to a more settled way of life based on food production (agriculture and herding), but stone continued for some time to be used for tools (such as ground axes, projectile points, and sickles).

The Paleolithic is traditionally divided into three major subdivisions: (1) the Early Paleolithic (also sometimes called the Lower Paleolithic) or Early Stone Age (ca. 2.6 Ma to 250,000 years ago); (2) the Middle Paleolithic or Middle Stone Age (ca. 250,000–30,000 years ago); and the Late Paleolithic (also Upper Paleolithic) or Later Stone Age (ca. 40,000–10,000 years ago). The "Lower"/"Middle"/"Upper" designations for the Paleolithic stages were developed in Europe in the late nineteenth and earlier twentieth centuries, based primarily on diagnostic artifact types and technological patterns observed in the stratigraphic and cultural sequences in various regions of Europe. More recently, with the appreciation that other parts of the world did not follow the precise cultural-historical sequence of Europe, many researchers have put less formal emphasis on these designations in favor of the more neutral terms "Early"/"Middle"/"Late" on a worldwide scale. This latter terminology will be used here.

For the first hundred years of Paleolithic research, these Paleolithic subdivisions were used to express a general chronological sequence (a relative chronology) without a firm sense of how many years ago each phase began or ended (an absolute chronology). During the past half-century, however, radiometric dating techniques have allowed the development of a more precise chronological framework for this Paleolithic sequence worldwide (see chapter "▶ Chronometric Methods in Paleoanthropology," Vol. 1), with approximate times for the beginning and end of each phase.

Change from one stage of the Paleolithic to the next, however, does not always entail an immediate or complete turnover in artifact types, though it does generally represent an obvious and perceptible shift in the types of artifacts dominating the archaeological tool assemblages and often a corresponding shift in the dominant methods used in making these tools. For instance, while modified flake tools are present at a number of Lower Paleolithic sites, they become the dominant artifact form, often with consistent or repeated shapes, at many Middle Paleolithic sites. There is also some regional variation in the absolute chronology of the sequence, with evident technological transitions in some regions occurring earlier or later than in other regions. For instance, the transition from the Middle Paleolithic/Middle Stone Age to the Late Paleolithic/Later Stone Age happens somewhat earlier in some regions than in others.

Perspectives on Early Stone Tools

The earliest prehistoric archaeological record is now approximately 2.6 Myr old, based on the recognition of flaked stone artifacts in securely dated deposits in East Africa. The fossil record of bipedal hominids, however, goes back at least 6 Ma, several Myr before the first appearance of stone tools (see chapter "▶ Role of Environmental Stimuli in Hominid Origins," Vol. 3). On the basis of modern primate analogs, especially from chimpanzees, a range of tools and tool-using behaviors might be postulated for hominid populations prior to 2.6 Ma. Such hypothetical early tool use likely involved highly perishable, organic raw materials that provide no enduring, visible archaeological record.

A handful of nonhuman species have been documented to show some minimal use of tools in the wild, including sea otters, birds (such as crows, finches, and Egyptian vultures), and even mud wasps (Shumaker et al. 2011). Aside from humans, however, the only other animals showing habitual use of a variety of tools for a variety of purposes are our closest living relatives, the chimpanzees (McGrew 1992). What is more, chimpanzee toolmaking and tool-using skills appear to be learned over several years, suggesting a simple culturally transmitted system.

We now know that there is variability among different chimpanzee groups in the sets of tools (see chapters "▶ Great Ape Social Systems", "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition", "▶ The Hunting Behavior and Carnivory of Wild Chimpanzees," Vol. 2, and "▶ Modeling the Past: Archaeology," Vol. 1) they commonly use, showing cultural variation among chimpanzees in their tool kits. Modern chimpanzee tool use includes nut cracking with stone and wood hammers and anvils, termite fishing, ant dipping with sticks or grass stems, and using chewed-up wads of leaves as sponges to obtain water or for self-cleaning. Although some chimpanzee tools consist of unmodified objects used for a particular task, chimpanzees do intentionally modify or shape some of their tools, such as the sticks and grasses used for termite fishing or ant dipping and the chewed leaves used as sponges.

Deliberately manufactured stone artifacts in the early archaeological record represent the earliest evidence of tool production by early hominids. As such, they reveal the development of a reliance on stone tool use in early hominid adaptation by at least 2.6 Ma. Although stone tool use may have been affected by seasonal, environmental, or other opportunities, the archaeological record reveals a consistent manufacture of stone tools that persisted from this time onward until recent times.

Early stone artifacts clearly indicate a number of interesting behavioral characteristics of these early hominids: they selected stone raw materials at specific locations, transported manufactured artifacts and unmodified stone from one place to another on the paleolandscape, and discarded artifacts (and sometimes parts of animal carcasses) in distinct concentrations at many localities some distance from the raw material sources. Moreover, the manufacturing process used to produce early stone artifacts is one that is not observed in any nonhuman animal, even among chimpanzees, highlighting the novelty of behavioral innovation in the early stone toolmakers. Although early stone tools are admittedly simple and do not show elaborate shaping, they represent clear evidence of a new and unusual behavior pattern: the deliberate, controlled fracture of rock through percussive blows.

Technological patterns seen in early stone artifacts indicate they were produced primarily through a technique sometimes called "free hand, hard hammer percussion." This involves hitting one rock (the hammer) against another (the core) to bring about controlled fracture of the core (called conchoidal fracture, as the shock waves can produce radiating, shell-like ripples in finer-grained materials) and produce numbers of sharp pieces called flakes, a process called flaking or knapping. Experiments have shown that the main objective of early stone tool making was likely the production of such sharp flakes to use as cutting tools. Thus, a primary tool in the early hominid tool kit was likely the sharp-edged flake, and many of the cores found at early sites were likely by-products of the toolmaking process (see chapter "▶ Modeling the Past: Archaeology," Vol. 1).

Early stone toolmaking hominids were consistently producing such fractured stones at a number of early site localities. Early Paleolithic sites often involve dozens of flaked cores and thousands of flake products. Analysis of early archaeological materials often reveals extensive, controlled flaking of cores, involving rotation and manipulation to produce a series of flakes from the same piece of stone. Such fine core manipulation and exploitation is observable at even the very earliest Stone Age sites at Gona in Ethiopia, showing consistent, controlled, and skillful flaking of cores by 2.6 Ma.

With such skillful flaking observable among early hominid toolmakers on the one hand and the diverse tool-using and toolmaking cultures observable in chimpanzees (McGrew 1992) on the other, a natural question is whether the production of early stone tools represents skills beyond those seen in other apes. Wild chimpanzees are known to have ca. 40 cultural traits, which can pattern geographically (Whiten et al. 1999). At the subspecies level, chimpanzee groups in closer proximity tend to share more of these cultural traits (Toth and Schick 2009; Whiten et al. 2009). Although chimpanzees are known to use stones as hammers and anvils in nut-cracking activities in West Africa, wild chimpanzee tool manufacture does not involve the intentional percussive flaking of stone, and wild chimpanzees have not developed sharp-edged tools for cutting in their assorted tool kits. It has been possible, however, to explore through experiments how comparable toolmaking skills of early hominids are to those of apes in captivity. An essential question in such experiments is whether the toolmaking skills of early hominids represent a significant departure from an ape "substrate" of toolmaking ability and what insights we might gain regarding early hominid cognitive abilities. Do early hominid toolmakers exhibit special cognitive or biomechanical skills or abilities,

Fig. 1 Kanzi, a bonobo (*Pan paniscus* or "pygmy chimpanzee"), flaking stone. Kanzi learned stone tool manufacture by modeling or imitation followed by years of trial and error, and he uses his tools to cut open a container to obtain food. His stone toolmaking skills have improved since the start of this experiment in 1990. Many of his artifacts resemble those found at Oldowan sites, although overall his flakes and cores still show some important differences from those found at Early Paleolithic sites

or do these emerge only much later in human biological and technological evolution? (see chapter "▶ Theory of Mind: A Primatological Perspective," Vol. 2).

Experiments were begun in 1990 teaching a bonobo (see chapters "▶ Great Ape Social Systems" and "▶ Primate Intelligence," Vol. 2) (pygmy chimpanzee), Kanzi (Savage-Rumbaugh and Lewin 1994), to make and use stone tools (Fig. 1) (Toth et al. 1993; Schick et al. 1999). The experiment involved introducing the use of a stone tool for cutting and retrieving a foodstuff, initial demonstrating (modeling) stone tool manufacture, and a subsequent period of trial-and-error learning on Kanzi's part in both the toolmaking and tool-using operations. This experiment has clearly shown that apes can become adept at some aspects of stone toolmaking. However, after more than 15 years of this experiment, some distinct technological differences have persisted in the bonobos' artifacts compared to artifact assemblages found at early Paleolithic sites (Toth et al. 2006; Toth and Schick 2009). Some of these differences appear to reflect lesser skill in the bonobo toolmaker, perhaps reflecting lesser cognitive appreciation of particular facets of the toolmaking process (such as flaking sharper edges of the core), although others are likely related to biomechanical differences in the hand and arm of the apes.

This experiment highlights how skilled and adept early stone hominids were in their stone toolmaking by the time of the earliest known archaeological occurrences 2.6 Ma. The skillfulness reflected in the earliest stone tools might suggest that even earlier stone technologies existed, yet undiscovered and perhaps rare on the paleolandscape, whose makers were not quite as proficient in flaking stone and who did not produce such a readily recognizable product. Or it may be that hominids were "preadapted" to efficiently flaking stone because of selection for other manipulative skills that were later transferred to stone knapping when the need arose. The ape stone tool making experiments give important clues as to what technological characteristics might be found in such hypothetical "Pre-Oldowan" technologies.

Early Paleolithic

The Early Paleolithic comprises a long time interval, between 2.6 Ma and approximately 250,000 years ago. It not only includes this extremely large span of human prehistory but also encompasses, over time, sites across huge geographical distances, from southern Africa to eastern Asia. During this period of more than 2.25 Myr, profound evolutionary changes occurred among hominids, and some marked changes are observed in the archaeological record in multiple parts of the Old World.

In Africa, where the Early Paleolithic is often referred to as the Early Stone Age, two industries have been recognized: (1) The first to appear, starting 2.6 Ma, the Oldowan industry (named after Olduvai Gorge in Tanzania), consists of stone industries containing simple cores and flaked pieces, along with some battered artifacts such as hammerstones and (2) starting between 1.7 and 1.5 Ma, or approximately 1 Myr after the onset of Oldowan technology, the Acheulean industry (named after the locality of St. Acheul in France) appears, with new distinctive artifact forms in the form of relatively large bifacial tools (handaxes, cleavers, and picks).

Oldowan

The Oldowan is the first recognizable archaeological record, with simple flaked and battered stone artifacts, sometimes found with cut-marked and broken animal bones, emerging around 2.6 Ma. Although similar types of simple lithic industries are found throughout time, archaeologists usually use a cutoff of around 1 Ma when referring to the Oldowan Industrial Complex. The Oldowan coexisted for several hundred thousand years with the Acheulean handaxes industries, starting about 1.76 Ma. Oldowan sites are known first from Africa and subsequently document the spread of hominids outside of Africa into parts of Eurasia, notably producing archaeological sites in the Near East, the Republic of Georgia, and eastern Asia. These sites are found especially in tropical and subtropical climatic regimes, in particular grassland/woodland environments.

At Dikika, Ethiopia, it has been argued that marks on surface bovid bones believed to date to 3.3 Ma were produced by stone tool-wielding hominids, in this case the contemporary *Australopithecus afarensis* (McPherron et al. 2010). Others, however, have argued that these marks could be produced by crocodile teeth (Njau 2012) or by trampling (Domínguez-Rodrigo et al. 2010). No stone tools have been found at this locality. Until new evidence comes to light, the claim of stone cutting tools from this time period should be regarded as unsubstantiated.

In East and North Africa, most Oldowan sites are open-air occurrences that are located along stream courses, in deltaic settings, or on lake margins. These were areas of close proximity to water and were depositional settings where sediments could build up over time. In South Africa, Oldowan artifacts are found in karstic limestone cave deposits and may have been carried there by hominids or brought in by natural forces such as slope wash or gravity. The high incidence of hominid bones in South African cave deposits (especially robust australopithecines) may be the result of predation and/or scavenging by carnivore such as leopards and hyenas.

Oldowan industries are contemporaneous with a number of bipedal hominid forms, including later australopithecines (see chapter "▶ The Species and Diversity of Australopiths," Vol. 3) (*Australopithecus garhi*, *A. aethiopicus*, *A. robustus*, and *A. boisei*), whose cranial capacities ranged from about 400 to 550 cm^3, and early forms of the more encephalized genus *Homo* (see chapter "▶ Evolution of the Primate Brain," Vol. 2) (*H. rudolfensis*, *H. habilis*, *H. ergaster/erectus*), whose cranial capacities ranged from about 600 to 850 cm^3. Although it is possible that all of these hominids used stone technology to a greater or lesser extent, many anthropologists believe that the genus *Homo* was probably the more habitual toolmaker and tool user, as its brain size almost doubles in the first million years of the Oldowan, while its jaws and teeth tend to diminish in robusticity. By 1 Ma, only *Homo ergaster/erectus* was known in the human paleontological record, while the australopithecines became extinct. Interestingly, *Homo ergaster/erectus* appears to have much more modern limb proportions and stature relative to earlier hominids and is the first form clearly identified outside of Africa (see chapters "▶ *Homo ergaster* and Its Contemporaries," "▶ Later Middle Pleistocene *Homo*," and "▶ Defining *Homo erectus*," Vol. 3).

Oldowan industries are characterized by simple technologies (sometimes called Mode 1) consisting of cores made on pebbles or chunks (choppers, discoids, polyhedrons, heavy-duty scrapers, facetted spheroids), battered percussors (hammerstones and battered spheroids), debitage (flakes and fragments), and retouched pieces (scrapers, awls, etc.) (Fig. 2) (Hovers and Braun 2009; Isaac 1989; Leakey 1971; Schick and Toth 2010; Toth and Schick 2006, 2009). Common raw materials include volcanic lavas, quartz, and quartzite. The most common techniques for producing Oldowan artifacts were hard hammer percussion and bipolar technique (in which the core to be flaked is set on a stone anvil and hit with a stone hammer). At Olduvai Gorge, some technological trends have been observed through time, with later Oldowan sites showing higher frequencies of such artifact classes as scrapers and battered spheroids and lower frequencies of choppers. These sites are sometimes assigned to a "Developed Oldowan," but this designation is more difficult to apply elsewhere.

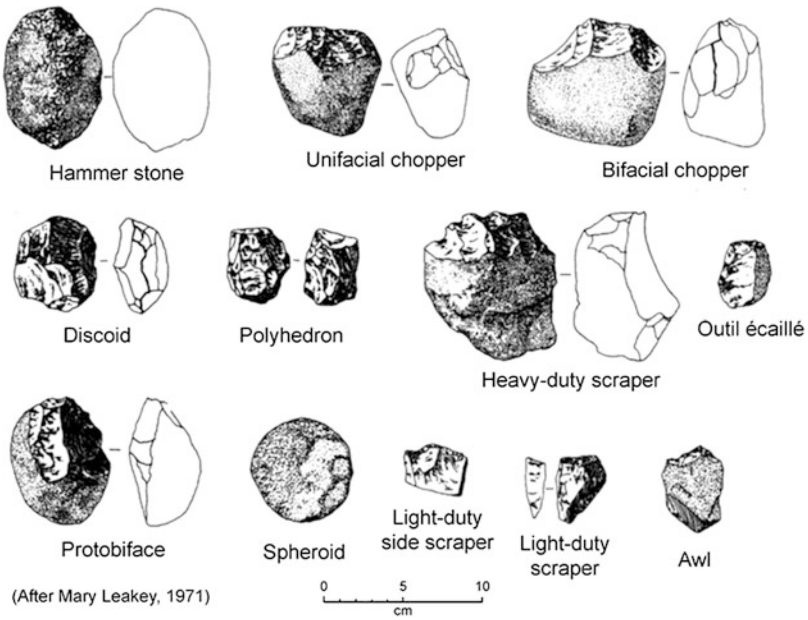


Fig. 2 Typical Oldowan artifacts found at Early Paleolithic sites. These are examples of flaked and battered stone artifacts found at Olduvai Gorge, with their common or conventional designations ("types") noted

Microwear patterns on a small sample of Oldowan tools suggest that flakes were used for animal butchery, woodworking, and cutting soft plant matter. Experiments in using stone tools (Fig. 3) have shown that Oldowan flakes can be used to efficiently process the carcasses of animals from the size of small mammals to elephants (Fig. 4) and stone hammers could easily break bones for access to nutritious marrow and skulls for brain tissue. Choppers could have been used to chop branches to make spears or digging sticks, although many such Oldowan core forms were probably by-products of flake production. It is likely that a rich range of perishable organic material cultures were also used, including containers of shell, horn, skin, or bark; wooden clubs and/or throwing sticks; wooden spears or digging sticks (Fig. 5); and horn or bone fragments as digging tools. In addition, a small sample of bone specimens from South African caves are polished and striated on their pointed end, suggesting that these may have been used as opportunistic digging tools to gain access to underground vegetable resources or insects such as termites.

Although evidence of fire has been found at a few Oldowan sites (in the form of reddened, baked sediments, burnt bones, or fire-cracked stone), it cannot be ruled out that natural agents, such as lightning strikes and brushfires, may have produced these fires. No clear architectural structures have been found at Oldowan sites, and it is possible that Oldowan hominids could have been sleeping in trees at night (perhaps building nests like chimpanzees) rather than on the ground, in order to

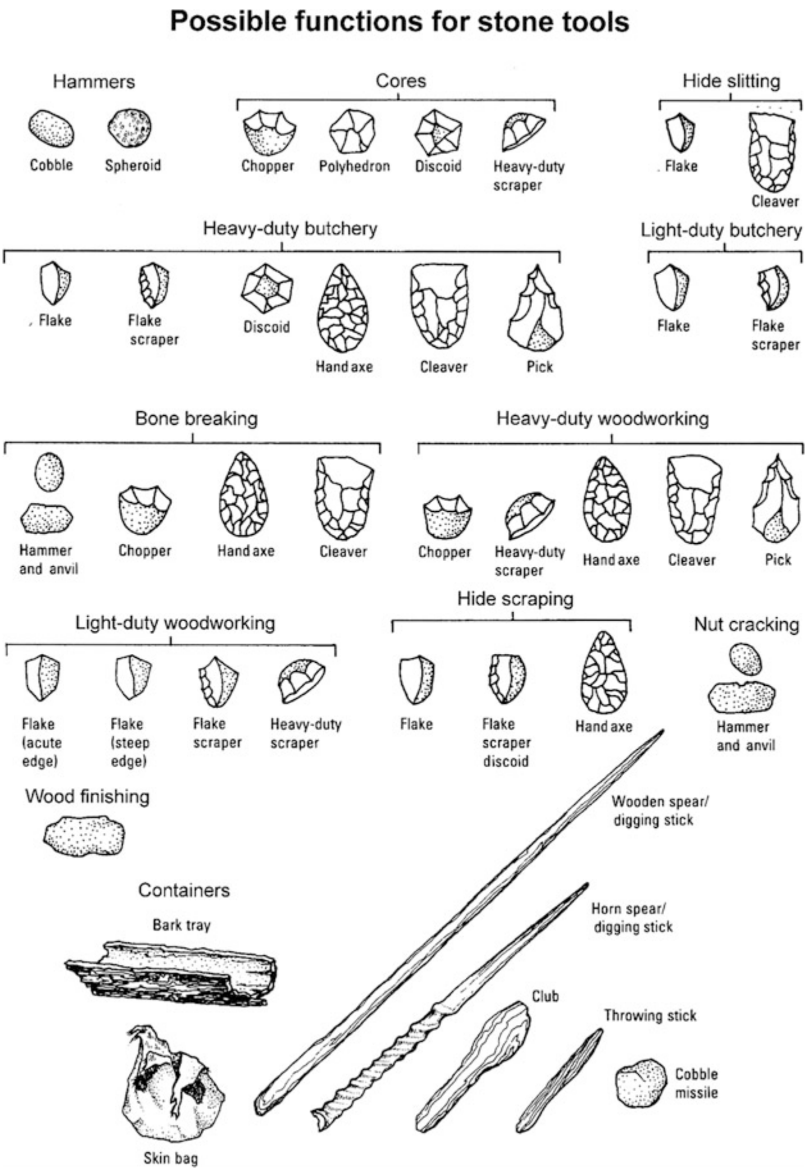


Fig. 3 Potential functions of Early Paleolithic artifacts, both Oldowan and Acheulean forms, based on experiments using tool replicas for various purposes

avoid predation by nocturnal carnivores (see chapters "▶ Evolutionary Biology of Ape and Monkey Feeding and Nutrition," "▶ Great Ape Social Systems," and "▶ The Hunting Behavior and Carnivory of Wild Chimpanzees," Vol. 2).

It seems clear that these Oldowan hominids were concentrating lithic material and animal bones at favored locations on the landscape (a pattern not seen in

Fig. 4 Butchery of an elephant, the world's largest terrestrial mammal, using simple Oldowan flakes (The elephant had died of natural causes)

Fig. 5 Sharpening a wooden branch with a simple stone flake. Such implements could have been used as spears, digging sticks, or skewers to carry meat resources

nonhuman primates today), but the precise behavioral patterns that formed these concentrations are still debated. Interpretations for these concentrations include home bases or central foraging places; favored places due to proximity to shade, water, or food resources; intentional stone caches; and scavenged carnivore accumulations. It is also possible that Oldowan sites formed through more than one behavioral pattern. Cut marks and percussion marks/fractures on bones show that hominids were accessing meat and marrow resources from animal carcasses obtained through scavenging or hunting. The modified bones at Oldowan sites typically come from animals ranging in size from small mammals to those weighing hundreds of pounds. This is a scale of carnivory that is not seen in the nonhuman primate world and was most likely greatly facilitated through the use of stone tools.

At present, there is debate as to whether hominids accessed larger animals through more marginal scavenging (getting the ravaged leftovers of carnivore kills) or, rather, had access to more complete carcasses through hunting or confrontational scavenging. In any case, the processing of larger animal carcasses could have significantly increased the dietary breadth (and thus survivorship and reproductive success) of Oldowan hominids, although the majority of Oldowan hominid diet was likely derived from plant foods such as fruits, berries, nuts, edible leaves, and underground storage organs (roots, tubers, corms, and rhizomes). Carrying devices may have facilitated the collection and transport of dietary items that could be consumed at a later time.

Important Oldowan localities include Gona, Fejej, and the Omo Valley in Ethiopia; East and West Turkana in Kenya; Olduvai Gorge in Tanzania; Sterkfontein and Swartkrans Caves in South Africa; Ain Hanech and El Kherba in Algeria; the lowest levels at ʻUbeidiya in Israel; and Dmanisi in the Republic of Georgia.

Acheulean

The Acheulean Industrial Complex is characterized by the presence of large bifacial handaxes, cleavers, and picks (sometimes called Mode 2 technologies), which are found from approximately 1.76 Ma to 250,000 years ago. The earliest known Acheulean sites are Kokiselei 4, West Turkana, Kenya, dated to 1.76 million years ago (Lepre et al. 2011), and Konso in Ethiopia, dated to 1.76 million years ago (Beyene et al. 2013). At Kokiselei four large cobbles of phonolite lava were flaked into crude handaxes and picks, while at Konso-Gardula, similar large picks and bifaces and unifaces were manufactured primarily from large flakes. Such handaxe/cleaver industries are contemporaneous and sometimes regionally co-occurring with the simpler Oldowan-like (Mode 1) industries. Acheulean and contemporaneous Mode 1 industries are found throughout Africa and Eurasia, but classic handaxe and cleaver assemblages are especially characteristic of Africa, the Near East, the Indian subcontinent, and Western Europe. Elsewhere, notably Eastern Europe and most of eastern Asia, simpler Mode 1, Oldowan-like technologies are found. This was a period of major climatic change, with numerous cold/warm oscillations that would have especially affected northern latitudes of Eurasia. For most of this period, hominids would have flourished only during the warmer periods in these northern latitudes. Hominids extended their range from grasslands and woodlands of tropical and subtropical regions to cooler, more temperate climates during this period (Fleagle 2010; Gamble 2005; Norton and Braun 2010; Shipton and Petraglia 2010).

Contemporaneous hominid forms (see chapter "▶ *Homo ergaster* and Its Contemporaries," Vol. 3) include *Homo ergaster/erectus* and the later, larger-brained *Homo heidelbergensis* (sometimes referred to as "early archaic *Homo sapiens*"). Cranial capacities range from about 800 to 1,400 cm^3, generally increasing over the time span of this period. In the early Acheulean, robust australopithecines (see chapters "▶ Analyzing Hominin Phylogeny: Cladistic Approach" and

"▶ The Species and Diversity of Australopiths," Vol. 3) (*A. robustus* and *A. boisei*) still existed, but most anthropologists do not regard these forms as plausible Acheulean toolmakers, and in any case they appear to have gone extinct by 1 Ma.

New elements in Acheulean industries (in addition to Mode 1, Oldowan-like artifacts that continue to be found) include handaxes, cleavers, picks, and knives (generically called "bifaces") made either on large flakes struck from boulder cores or on larger cobbles and nodules. A range of well-made retouched tools, such as side scrapers, awls, and backed knives, are also common. Frequently used raw materials include fine-grained lavas, quartzites, and flints. Earlier, cruder bifaces were produced by hard hammer percussion (Fig. 6), while later more refined bifaces

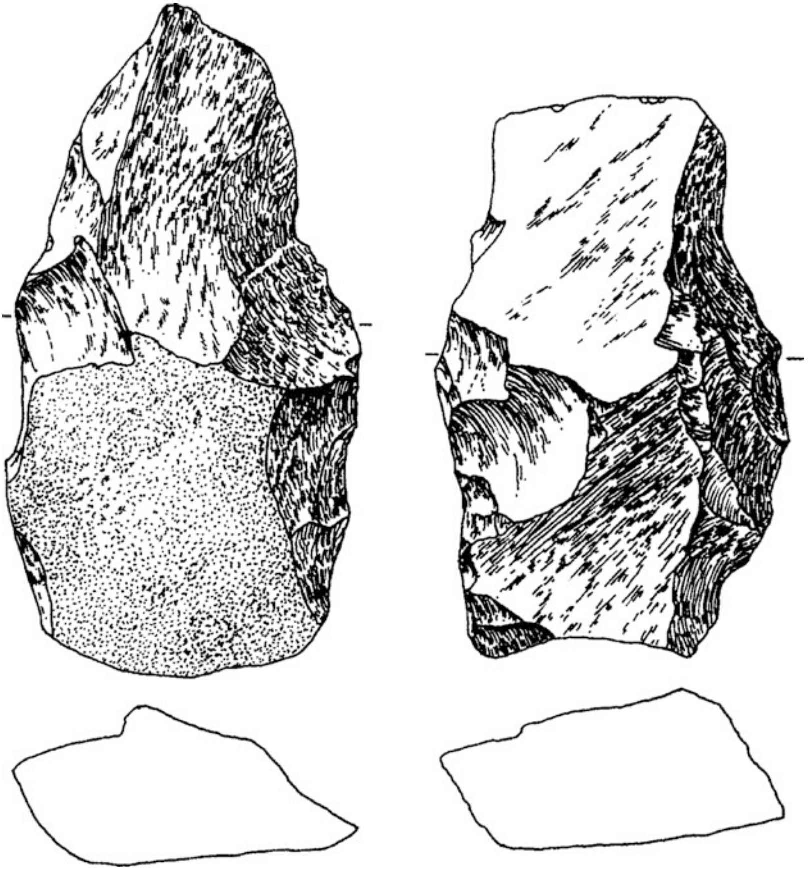
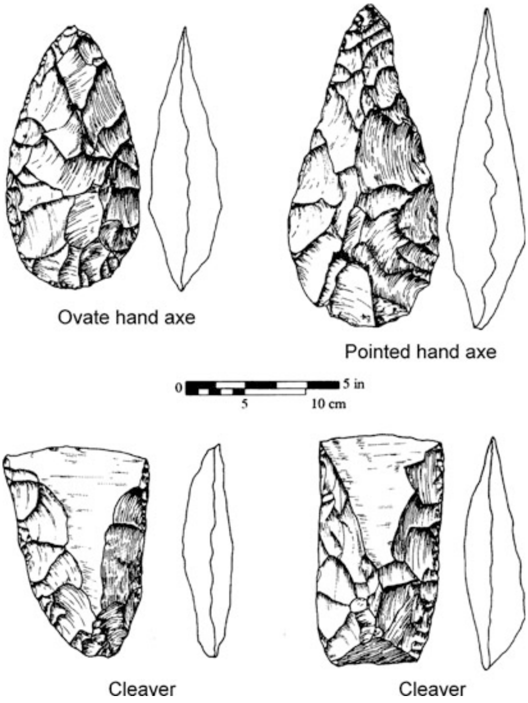


Fig. 6 Early Acheulean tools: relatively crude handaxe (*left*) and cleaver (*right*), approximately 1.4 Myr old. These artifact forms, made on large flakes or cobbles, show definite shaping to leave a sharp working edge, especially toward the tip end of the handaxe and the bit of the cleaver, with the lower part of the tool shaped or left natural to serve as a handle. They usually show some, though relatively low, degree of symmetry in their plan view and their cross-section and were made by hard hammer percussion

Fig. 7 Late Acheulean tools: beautifully made, highly symmetrical handaxes and cleavers typical of the latter part of the Acheulean, approximately 400,000 years old. These forms clearly show more cognitive complexity, craftsmanship, and probably an aesthetic sense hundreds of thousands of years before the first representational art



were probably finished by the soft hammer technique, in which a softer material, such as wood, bone, ivory, antler, or even soft stone, was used as a percussor, producing thinner, more invasive flakes (Fig. 7). Prepared core techniques, notably the Levallois tortoise core technique (in which a large, predetermined flake is removed from the upper surface of a discoidal core) and, more rarely, early blade production, are found in some later Acheulean industries. Sharpened wooden spears are known from later Acheulean times, as at Schöningen in Germany (see chapter "▶ Modeling the Past: Archaeology," Vol. 1) and Clacton in England, suggesting that more formal hunting weaponry was established as part of a regular subsistence pattern by at least this time if not earlier.

The fact that Acheulean and contemporaneous hominids successfully occupied cooler, more temperate latitudes suggests that they were better adapted to such cooler conditions. Use-wear patterns on side scrapers indicate that many of these tools were used to scrape hides, strongly suggesting that animal skins were being used for simple clothing, blankets, and/or tent or hut coverings. Evidence of fire in the form of charcoal or ash layers is occasionally seen in later Acheulean times but is by no means widespread in the archaeological record during this period. There is no definitive evidence of architectural structures during Acheulean times, although arguments have been made in this regard. Sites are found in numerous caves and rock shelters as well as many open-air sites.

Handaxes and cleavers, in particular, indicate the ability to impose bilateral symmetry on lithic materials. This clearly shows higher cognitive abilities and motor skills than are manifested in the Oldowan. Even modern humans who learn to make stone tools normally require considerable apprenticeship before they can produce well-made handaxes and cleavers. Although there is a wide range of handaxe forms through time and space, it is common that at certain Acheulean sites, there are recurrent shapes and sizes, as if there were stylistic norms of production among their makers. Presence of ocher at some sites and, occasionally, incised bone may indicate the emergence of proto-symbolic behavior as well.

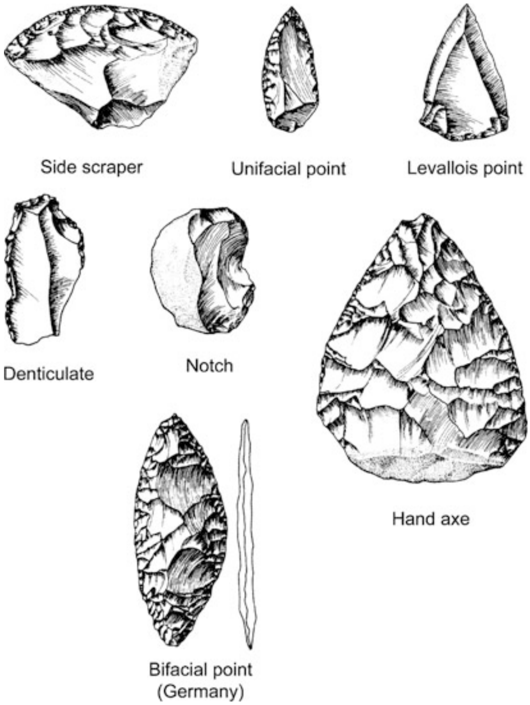
Important Acheulean sites/localities include Konso-Gardula, Middle Awash, Melka Kunture, and Gadeb in Ethiopia; Olduvai Gorge and Peninj in Tanzania; Olorgesailie and Isenya in Kenya; Kalambo Falls in Zambia; Elandsfontein and Montagu Cave in South Africa; Ternifine in Algeria; ‘Ubeidiya and Gesher Benot Ya’aqov in Israel; Swanscombe, Hoxne, and Boxgrove in England; Saint-Acheul and Terra Amata in France; and Torralba and Ambrona in Spain. Important contemporaneous Mode 1 localities include Atapuerca (TD6) in Spain, Arago Cave in France, Clacton in England, Bilzingsleben and Schöningen in Germany, Vértesszölös in Hungary, Isernia in Italy, and the Nihewan Basin and Zhoukoudian (“Peking Man”) cave in China.

It has recently been argued (Wilkins et al. 2012) that stone points from Kathu Pan 1, South Africa, believed to date to ca. 500,000 years ago, could have functioned as hafted spear points, based upon the morphology of the artifacts and edge damage. These artifacts are associated with a stone tool industry, often referred to as the “Fauresmith” that includes handaxes and is considered by some to be transitional between the Acheulean and the Middle Stone Age. If this argument is valid, this would put the origins of hafted technologies several hundred thousand years before the first widely accepted evidence of hafting (see chapters “▶ Modeling the Past: Archaeology,” Vol. 1, and “▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories,” Vol. 3). Kathu Pan 1 also shows evidence of systematic blade production, another trait which tends to appear in the archaeological record in later times (Wilkins and Chazan 2012).

Middle Paleolithic/Middle Stone Age

The Middle Paleolithic industries of Europe, the Near East, and North Africa (sometimes called the “Mousterian” after the site of Le Moustier in France) and Middle Stone Age industries of sub-Saharan Africa are found between approximately 250,000 and 30,000 years ago. They are found in tropical, subtropical, temperate, and even periglacial climatic regimes. During this time, hominids extended their ranges to most environmental zones of Africa and Eurasia except harsh deserts, the densest tropical forests, and extreme northern or arctic tundras.

Fig. 8 Middle Paleolithic tools: numerous retouched flake tools, such as side scrapers, points, and denticulates, were made on flake blanks, some struck from prepared cores. It is possible that some of these points were hafted to wooden shafts as thrusting or throwing spears



It appears that hominids were somehow able to cross the water between Southeast Asia and Australia and then attached to New Guinea and Tasmania, by late in this period. Contemporary hominid forms include those often designated as archaic *Homo sapiens* (including the Neanderthals of Europe and the Near East) and anatomically modern humans.

Handaxes and cleavers tend to be less common (although toward the end of the Middle Paleolithic of Western Europe, smaller, well-made handaxes are found), and the emphasis in these stone industries is on retouched forms made on flakes (such as side scrapers, denticulates, and points) that become numerous in many of these assemblages (Fig. 8). Hard hammer and soft hammer techniques were common during this period. Many of these industries exhibit prepared core methods, notably the Levallois technique for more controlled production of flakes, points, and sometimes blades. Wooden spear technology continues from the Acheulean (as seen at Lehringen, Germany, where a spear with a fire-hardened tip was associated with an elephant carcass), and stone points with tangs or thinned bases suggest that these forms may have been hafted onto spear shafts, suggesting the development of composite tools. Rare bone points are also known from this time.

Fire and hearth structures are much more common during this period, although clear architectural features outlined by stones or bones are rare. Sites are numerous in caves and rock-shelters, as well as open-air sites on plateaus and along river floodplains.

Occasional perforated and grooved shells and teeth at a few sites imply the emergence of some personal adornment and, along with the infrequent presence of ocher as well as a number of well-documented burials, suggest at least some symbolic component to hominid behavior during this period of the Paleolithic (McBrearty and Brooks 2000).

Important Middle Paleolithic/Middle Stone Age sites include Combe Grenal, Pech de L'Azé, Le Moustier, La Quina, and La Ferrassie in France; Krapina in Croatia; Cueva Morin in Spain; Tabun, Skhūl, Kebara, Amud, and Qafzeh in Israel; Shanidar in Iraq; Dar es-Soltan in Morocco; Bir el Ater in Algeria; Haua Fteah in Libya; Kharga Oasis in Egypt; Diré-Dawa, Omo-Kibish, and Middle Awash in Ethiopia; Enkapune Ya Muto, Prospect Farm, and Kapthurin in Kenya; Kalambo Falls and Twin Rivers in Zambia; and Florisbad, Border Cave, Klasies River Mouth Cave, and Die Kelders Cave in South Africa.

Late Paleolithic

The Late Paleolithic (often called Upper Paleolithic in Europe and Later Stone Age in Africa) is found between 40,000 and 10,000 years ago, at which time the last glaciation receded. This period of human prehistory overlaps and is contemporaneous with the end of the Middle Paleolithic/Middle Stone Age in some regions. During this time, humans inhabited tropical, subtropical, temperate, desert, and arctic climates; occupied present-day Australia, New Guinea, and Tasmania after crossing significant bodies of water; and, late in this period, spread to the Americas via the Bering Straits (see chapters "▶ The Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia" and "▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories," Vol. 3). Late Paleolithic industries are almost always associated with anatomically modern humans (*Homo sapiens sapiens*), but some early Upper Paleolithic sites in Europe are also contemporaneous with the last populations of Neanderthals (see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3) there.

Late Paleolithic stone industries are often characterized by blade technologies, elongated flakes produced by soft hammer or indirect percussion, in which a punch is placed on the edge of a blade core and struck with a percussor. These blades were then made into a variety of tool forms, including end scrapers, burins, and backed knives (Fig. 9). Some Late Paleolithic technologies emphasized bifacial points, such as the Solutrean of Spain and France and the Paleo-Indian occurrences of the New World (Clovis and Folsom) (see chapter "▶ The Dentition of American Indians: Evolutionary Results and Demographic Implications Following Colonization from Siberia," Vol. 3). Such points may have been produced by soft hammer technique or by pressure flaking, in which small flakes are detached by directed pressure rather than by percussion. Some raw materials appear to have been heat treated to make them easier to work. Other Late Paleolithic technologies emphasized bladelets (small blades) and geometric microliths, which were hafted as composite tools into a range of projectiles and cutting tools. These microlithic

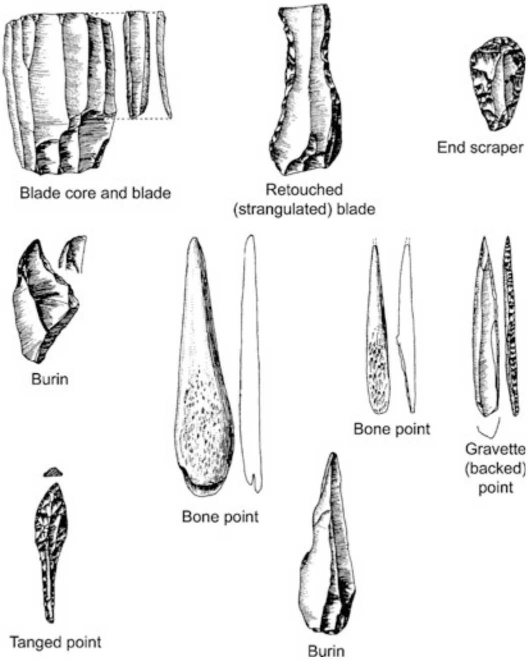


Fig. 9 Late Paleolithic tools: tools made on blades struck from prepared cores were important components of these technologies, made into such forms as end scrapers, burins, and points, as were formal tools shaped from bone, antler, and ivory

technologies are characteristic of the Later Stone Age of Africa as well as some parts of central and eastern Asia.

A diagnostic element of many Late Paleolithic industries is an emphasis on nonlithic materials for tools, including bone, antler, and ivory, made into a range of artifact forms such as points, needles, spear-throwers, shaft straighteners, and harpoons. Hooked spear-throwers are essentially mechanical devices to increase the velocity and/or distance of a projectile, and thus represent a significant advance in hunting technology or weaponry. The small size of some points and microliths toward the end of the Late Paleolithic suggest the development of bow and arrow technology, and arrows are preserved at Stellmoor, Germany.

Several human sculptures from the Late Paleolithic suggest clothing such as hooded parkas, headdresses, and aprons. The development of bone and antler needles also suggests that sewed clothing was common after 20,000 years ago, and recently discovered impressions on fired clay fragments from the Czech Republic indicate woven textiles, presumably of plant material.

Controlled use of fire appears to be a universal trait during this period, with hearths sometimes lined with stones. Architectural features are much more common than in earlier periods, with hut structures delineated by stone or bone patterns, by postholes, and sometimes with hearth structures and other apparent activity areas within (such as toolmaking or tool-using). Sites tend to be more numerous and have denser concentrations of materials, suggesting larger populations and more regular habitation of sites.

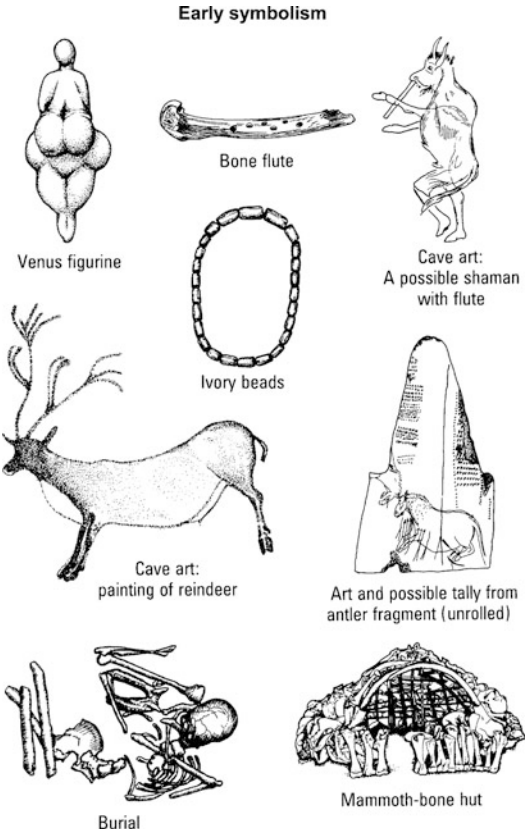


Fig. 10 Examples of probable symbolic behavior in Late Paleolithic times, expressed in art, personal adornment, music, notation, burial, and possibly more formal architecture

Relatively late in the time span of the Late Paleolithic, the first evidence of human occupation of the Americas appears. The most widespread evidence is attributed to the Clovis culture, characterized normally by fluted spear points and often associated with mammoth remains, dating to ca. 13,500–13,000 years ago. Several sites may predate the Clovis in the Americas by several thousand years (Meltzer 2010).

One of the most distinctive characteristics of the Late Paleolithic is the proliferation of symbolic expression in art and personal adornment (Fig. 10). This can be seen in the naturalistic representation of animals and, more rarely, humans in painting and sculpture as well as in the more abstract geometric designs. A variety of media were employed for artistic expression, including use of charcoal, pigment paints, antler, bone and ivory, and clay, as well as a diversity of techniques, including drawing, painting, engraving, carving, and modeling. Personal adornments are sometimes numerous, manifested in beads or pendants of shell, bone, tooth, antler, ivory, and stone. This proliferation of symbolic expression, best seen in the European Upper Paleolithic, has sometimes been referred to as the “Creative Explosion.” Some of these artistic manifestations, particularly paintings, drawings, and engravings, are located in deep, hard-to-access recesses of caves, suggesting a ritualistic and religious aspect to this symbolism. In view of the complexity of the material culture of this period and its well-developed symbolic component, it is likely that modern human language abilities were fully developed by this time, if not before.

Late Paleolithic burials are more common and more elaborate than in the Middle Paleolithic. Men, women, and children were sometimes interred with rich grave goods, including stone tools, jewelry, and bone/antler/ivory artifacts. Again, this suggests an important symbolic component and a probable belief in an afterlife, in other words, something akin to a spiritual belief and a religion.

Important sites include Lascaux, Pincevent, La Madeleine, Abri Pataud, Cro-Magnon, Solutré, Chauvet, and Laugerie Haute in France; El Castillo, Altamira, and Parpalló in Spain; Dolní Věstonice in the Czech Republic; Vogelherd in Germany; Istállóskö in Hungary; Willendorf in Austria; Kebara Cave in Israel; Ksar Akil in Lebanon; Kostienki and Sungir in Russia; Mezin and Mezhirich in Ukraine; Mal'ta in Siberia; Zhoukoudian Upper Cave in China; Lukenya Hill in Kenya; Mumba Cave in Tanzania; Nelson Bay Cave, Die Kelders, Elands Bay Cave, and Wilton, in South Africa; Haua Fteah in Libya; Lake Mungo in Australia; and Blackwater Draw in New Mexico (North America).

Conclusion

The earliest evidence of hominid technology dates to between 2.6 and 2.5 Ma in the Ethiopian Rift Valley. The Oldowan, characterized by simple cobble cores, flakes, retouched flakes, and battered percussors, is associated in time with later australopithecines and early forms of larger-brained hominids assigned to the genus *Homo*. Cut marks on fossil mammalian bones and hammerstone fracture of long bones indicate that one aspect of these early technologies was the processing of animal carcasses.

By 1.8–1.7 Ma, the prehistoric record documents the emergence of *Homo ergaster/erectus* and the early Acheulean, characterized by new artifact forms such as handaxes, cleavers, and picks. The first hominid migrations out of Africa and into Eurasia are documented at the same time. Later Acheulean sites, ca. 500–250 Ka, are often characterized by better-made and more symmetrical handaxes and cleavers and are associated with *Homo heidelbergensis*. Handaxe industries are known for much of Africa, the Near East, Western Europe, and the Indian subcontinent. In much of Eastern Europe and East Asia, contemporary hominid populations were producing simpler cobble cores and a range of retouched flake tools.

The Middle Stone Age/Middle Paleolithic emerges around 250 Ka, usually characterized by prepared core technologies (e.g., Levallois cores, flakes, and points), side scrapers, denticulates, and retouched points. In Africa these industries are associated with larger-brained archaic forms (sometimes assigned to *Homo helmei*) and early anatomically modern humans. In the Near East, such industries are associated with Neanderthals and modern humans. In Europe the Middle Paleolithic appears to be exclusively associated with Neanderthals. In East Asia during this time, the lithic industries are usually simpler core/flake/retouched flake industries, associated with archaic forms of hominids. Evidence of fire becomes very common during this period.

The Late Paleolithic (Upper Paleolithic, Later Stone Age) emerges in the Old World in the last 50,000 years. Industries are often characterized by blade production, blade tools such as backed knives, end scrapers, and burins, and a range of unifacial and bifacial point styles. For the first time, materials such as bone, antler, and ivory (and presumably a very rich wood technology) became major raw materials for tools. Architectural features such as hut structures and well-made hearths became common for the first time. The first representational artwork was produced on cave walls in the forms of paintings and engravings as well as mobiliary sculpture and engraving.

During the last glaciation, modern humans reached Australia by 40 Ka and the Americas by at least 15 Ka. Around the world, stone industries document a greater variability over time and space, suggesting stronger regional cultural rules regarding material culture and more innovation and technological change over time. With more complex technologies and adaptive patterns, humans were able to occupy extreme environments such as dense tropical forests, arid deserts, and frigid tundras. In a number of places in the Near East, Africa, East Asia, Oceania, and North and South America, these Paleolithic foraging societies slowly emerged as sedentary farmers, and then in some of these places, complex societies emerged as "civilizations" with urban centers.

The Paleolithic lasted over two-and-a-half million years and, in terms of duration, covers well over 99 % of human technological history. It is no exaggeration to say that the human lineage is a product of its Paleolithic past and that the modern human condition, characterized by industrialization, farming, urban life, and ever-increasing networks of communication and globalization, is firmly rooted in its Stone Age past.

Cross-References

- ▶ Chronometric Methods in Paleoanthropology
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ Defining *Homo erectus*
- ▶ Defining the Genus *Homo*
- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Geological Background of Early Hominid Sites in Africa
- ▶ *Homo ergaster* and Its Contemporaries
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Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia

Nicholas J. Conard

Contents

Abstract

This chapter examines large-scale patterns of behavioral change that are often viewed as indicators for the advent of cultural modernity and developed symbolic communication. Using examples from Africa and Eurasia, the chapter reviews patterns of lithic and organic technology, subsistence, and settlement as potential indicators of modern behavior. These areas of research produce a mosaic picture of advanced technology and behavioral patterns that come and go

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N.J. Conard
Eberhard–Karls–Universität Tübingen, Institut für Ur– und Frühgeschichte, Abteilung Ältere Urgeschichte und Quartärökologie, Tübingen, Germany

Senckenberg Center for Human Evolution and Paleoenvironment, Tübingen, Germany
e-mail: nicholas.conard@uni-tuebingen.de

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during the late Middle and Late Pleistocene. Based on these data the emergence of modern behavior, as seen in the archaeologically visible material record, appears to be gradual and heterogeneous in space and time. During the early part of the Late Pleistocene, personal ornaments in the form of perforated seashells are documented in southwestern Asia and northern and southern Africa. By about 40,000 years ago (Ka), a diverse array of personal ornaments are documented across the Old World in association with Neanderthals and anatomically modern humans. These include both modified natural objects and fully formed ornaments. The timing and distribution of the appearance of figurative art, mythical imagery, and other classes of artifacts including musical instruments point to a more punctuated development of fully modern behavior during the middle of the Late Pleistocene and certainly no later than 40 Ka. Due perhaps in part to the long and intense history of research, much, but by no means all, of the relevant data come from Europe. Early figurative art from the Aurignacian of southwestern Germany, northern Italy, Austria, and southern France provides undisputed evidence for fully developed symbolic communication and behavioral modernity. This chapter also discusses some of the hypotheses for the development and spread of cultural modernity and rejects a strict monogenetic model in favor of a pattern of mosaic polycentric development. This chapter highlights the need for new refutable, regional and superregional hypotheses for the advent and spread of behavioral modernity.

Introduction

The question of when in the course of human evolution hominids became like ourselves has been at the center of several decades of productive debate in paleoanthropology. Reduced to the most fundamental level, the appearance of anatomical and behavioral modernity is a question of at what time in the course of evolution hominid anatomy and behavior fall within the variability documented in recent societies. The key component of fully modern cultural behavior is communication within a symbolically organized world and the ability to manipulate symbols in diverse social and economic contexts.

This chapter will not address the development of modern human anatomy; here, I consider some of the key evidences for the evolution of complex behavioral systems. While there is no consensus about when modern behavior can first be identified in the archaeological record, by no later than about 40 Ka, various finds documenting the production of diverse ornaments, musical instruments, figurative representations, and mythical imagery provide undisputed evidence for cultural modernity. These and other archaeologically visible indicators of cultural modernity point to a patchy development of complex cultural behavior and symbolic communication across the Old World. While regional patterning is becoming increasingly visible (Delporte 1998; McBrearty and Brooks 2000; Bon 2002; Conard and Bolus 2003; Hovers and Belfer-Cohen 2006; Texier et al. 2010; d'Errico and Stringer 2011; Porraz et al. 2013), the current data on this topic include an uneven distribution of evidence that has been put through a selective taphonomic filter and that reflects diverse regional histories of research. These biases hinder the location of convincing centers of origin and dispersal for many of the key features considered here.

At present, we see diverse points of view regarding the origins of behavioral modernity, and current interpretations include but are not limited to the following models: (1) gradual African origin (McBrearty and Brooks 2000), (2) coastal origin in connection with new dietary patterns during the early Late Pleistocene (Parkington 2001), (3) punctuated late African origin (Klein 2009; Klein and Edgar 2002), (4) gradual origins across multiple human taxa and multiple continents (d'Errico et al. 2003), and (5) relatively late origins among multiple human taxa, including Neanderthals' own Upper Palaeolithic revolution (Zilhão 2001, p. 54). Here, I argue for a mosaic polycentric advent of behavioral modernity (Conard 2008). The evolution toward behavioral modernity accelerated in the middle of the Late Pleistocene, and culturally modern behavior with diverse regional signals and local innovations can be seen in many parts of Africa, Europe, Asia, and Australia between 30 and 45 Ka. While archaic and modern humans must have interacted in many regions in the context of diverse social and ecological settings, ultimately modern humans were at a demographic advantage in all regions and replaced archaic humans with relatively little interbreeding (Prüfer et al. 2013; Sankararaman et al. 2014).

This chapter reviews some of the evidence for advanced cultural behavior and argues for a highly variable pattern of development depending on specific historical and evolutionary contingencies. The development of modern behavior does not in my view represent a one-time-only quantum leap, but a complex pattern of innovation, spread, and local extinction of new traits through cultural selection and social reproduction. Social, technological, and linguistic reproductions through learning are fostered by the biological success of the members of societies, but are not only driven by demographic growth. Demographic trends and complex patterns of intra- and intersocietal contacts led to mosaic patterns of cultural development that result from specific historical and ecological events and processes during the Pleistocene. The current archaeological record provides glimpses of these evolutionary processes, but it would be naive to think that our current data on the fleeting material remains of the development and spread of behavioral modernity provide a one-to-one indication of where and when advanced technology, highly developed patterns of settlement and subsistence, ornaments, music, and abstract and figurative representation evolved. The question of why fully modern cultural behavior evolved is still more difficult to answer, but recent years have begun to see attempts to address the thorny questions of causality (Klein 2009; Parkington 2001; Shennan 2001; Lewis-Williams 2002; Conard and Bolus 2003; Jerardino and Marean 2010; Kuhn and Hovers 2013). Much more work is needed that addresses the potential causes of cultural evolution and develops testable hypotheses. In this context, monocentric and polycentric models need to be formulated and tested explicitly.

Turning to the more mundane aspects of archaeology, it is necessary to stress the ambiguities and problems with dating sites in excess of 40,000 years. Radiocarbon dating, the strongest tool for dating Later Stone Age (LSA) and Upper Paleolithic assemblages, begins to reach its limits in the period before 40 Ka. Here, several factors come into play. In this period, in excess of seven radiocarbon half-lives, contamination becomes a serious problem. The isolation of preserved collagen in bones and similar problems related to sample preparation become more problematic than in younger periods (Higham 2011). Also, the physics of the AMS and beta counting become more challenging as minimal contamination begins to affect the results more strongly and the uncertainties related to the chemistry and instrument background become significant. Equally important is the wealth of evidence that there are major fluctuations in radiocarbon levels, probably in connection with variations in production due to magnetic excursions (Voelker et al. 2000; Beck et al. 2001; Conard and Bolus 2003; Hughen et al. 2004). These factors tend to make radiocarbon ages underestimate the calendar age of archaeological materials in excess of 30,000 years (Higham 2011; Higham et al. 2012).

Other methods, including luminescence dating, have great potential for sorting out the chronology of the emergence of modern human anatomy and behavior, and the prospects for gaining improved chronological control for the later stages of human evolution are excellent (Richter et al. 2000; Jacobs et al. 2003a, b, 2008; Tribolo et al. 2013).

This presentation will of necessity be brief and in no way attempts to be encyclopedic. Instead, I consider examples to illustrate the overall pattern of behavioral evolution. These examples are often drawn from regions where I have worked and know the data best. The subject matter is divided into two main sections. The first deals with the nuts and bolts of Paleolithic archaeology and focuses on lithic and organic artifacts and patterns of subsistence and settlement. The second section deals more with data that provide more direct access to the Paleolithic world of symbols, beliefs, and communication and reviews evidence for burials, ornaments, figurative and nonfigurative representation, and music as a means of defining modern cultural patterns. In general, the results from a review of the latter kinds of evidence give a better indication of the origins of behavioral modernity. My concern here is not in developing trait lists or single signatures for modernity, but rather to look at the evolutionary contexts of diverse classes of data that may help us to identify patterns of behavioral evolution. Other similar reviews of this evidence at different geographic scales can be found in a number of publications and should be consulted along with the primary references for further details (Deacon and Deacon 1999; McBrearty and Brooks 2000; d'Errico 2003; d'Errico et al. 2003; Conard 2004a; Hovers and Belfer-Cohen 2006; Klein 2009; d'Errico and Stringer 2011). Finally, many of the chapters in this volume present up-to-date information that is of central importance for defining the evolution of modern behavior.

Technology, Settlement, and Subsistence as Measures of Modernity

Lithic Technology

Stone artifacts are a physically robust class of artifacts and often survive the numerous potential forms of taphonomic destruction. In this regard, they are a major source of data on early human behavior. In many Paleolithic settings, stone artifacts are the most abundant class of anthropogenically altered material. These attributes of lithic artifacts make them the most important means of defining Paleolithic cultural groups. Thus, if specific lithic artifacts can be shown to provide an indication of modern cultural behavior, scholars could use such finds as indicators of modernity.

Despite attempts to define linear and cladistic systems for the evolution of stone tools (Foley 1987; Foley and Lahr 2003), lithic technology is based on learned behavior and is not directly transmitted biologically. Thus, it comes as little surprise that new forms of lithic technology come and go over the more than two-million-year-old Paleolithic record. Oldowan technology is the most common form of flint knapping at the pyramids of Giza (Conard 2000), and this simplest of knapping approaches comes and goes throughout the Stone Age. Many other knapping technologies also come and go over the last several hundred thousands of years that are the backdrop for the development of anatomical and cultural modernity. Hand axes, Levallois technology, blade technology, and other elements of stone knapping come and go and do not provide certain indicators of behavioral modernity.

Additionally, the ethnographic record points to the problems associated with viewing lithic technology as a clear indicator of levels of cultural evolution. Subrecent ethnographic sources document cases of hunter-gatherers in regions including, for example, parts of Australia and Tierra del Fuego, who used Stone Age technologies that would leave no traces of behavioral modernity. These groups were undeniably modern humans and highly developed in respect to their linguistic skills and their ability to manipulate symbols, yet the lithic technology and the archaeologically visible material culture would leave no traces of this modernity.

Lithic technology provides no simple solution to the problems related to identifying modernity. Even blades, which were once seen as clear indicators for behaviorally modern Upper Paleolithic and Later Stone Age cultures, have been demonstrated in diverse contexts in Africa, the Near East, and Europe (Rust 1950; McBurney 1967; Besançon et al. 1981; Singer and Wymer 1982; Conard 1990, 2012; Révillion 1994; McBrearty and Brooks 2000; Locht 2002; Meignen 2011; Wojtczak 2011; Fig. 1). These blade-based assemblages date to the second half of the Middle Pleistocene and the Late Pleistocene and include technologies based on Upper Paleolithic platform cores and non-Levallois and Levallois blade production.

Lithic assemblages document a heterogeneous pattern of development, with forms coming and going across the Old World. While in Europe there is doubtless a difference between Middle and Upper Paleolithic assemblages, many forms typically associated with the Upper Paleolithic appear in earlier periods, and it is becoming increasingly clear that the variability documented by Bordes (1961) in the Middle Paleolithic of southwestern France reflects only a small portion of the overall lithic variability. Many regions of Europe (Bosinski 1967, 1982; Conard and Fischer 2000) show a diverse pattern of cultural development that is analogous to that documented in Africa (Clark 1982, 1988; McBrearty and Brooks 2000). Also in the Near East, the early Middle Paleolithic includes lithic assemblages such as Yabrudian and Humalian, and the later Middle Paleolithic is characterized by

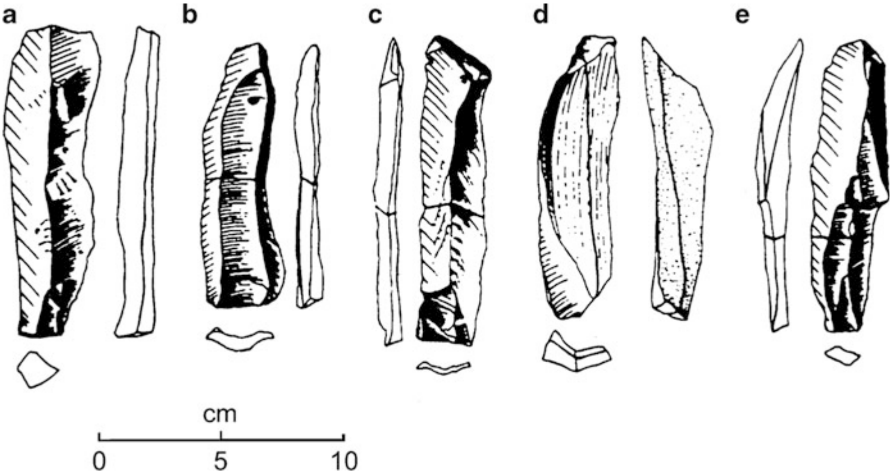


Fig. 1 Kapthurin Formation, Kenya. Late Middle Pleistocene blades ca. 250,000 years old (After McBrearty and Brooks 2000)

Levalloisian assemblages that were made by both Neanderthals and anatomically modern humans (Shea 2003). The latter observation demonstrates how tenuous the link is between anatomical and cultural evolution.

As Bosinski (1982), Clark (1982, 1988), and others have long pointed out, the Middle Stone Age (MSA) and Middle Paleolithic are marked by the growth and increased visibility of local traditions. The frequently made suggestion that lithic technology from these periods is static or even boring strikes me as incorrect. In many areas where high-quality data are available, MSA and Middle Paleolithic assemblages show considerable diversity. The development of local traditions appears to increase with time in some areas of Africa and Eurasia (Bosinski 1967; Conard and Fischer 2000; Wadley 2001; Jöris 2002; Conard et al. 2012; Porraz et al. 2013), but these trends are, to a certain extent, a reflection of the improved quality of data that results from both better chronological control and more numerous assemblages per unit time. Researchers who try to define variability must consider the quality and density of the available data. In general, early periods of the MSA and Middle Paleolithic have provided less data suitable for addressing these questions than the later phases of these periods or the LSA or Upper Paleolithic. Thus, it is not surprising that, in general, assemblages from more recent periods document more technological and typological variation than samples from earlier periods.

The complexity of Middle Paleolithic and MSA lithic technology is highly variable, but at times advanced. Hafting and composite tools have been documented directly and indirectly in many regions. In Africa, we can consider the standardized-backed forms from Howiesons Poort assemblages to be strong candidates for hafting, as well as numerous point assemblages of the Late Pleistocene and perhaps the Middle Pleistocene (Singer and Wymer 1982; McBrearty and Brooks 2000; Lombard and Phillipson 2010; Fig. 2). In southwestern Asia, Shea (1988, 1993, 1998) has

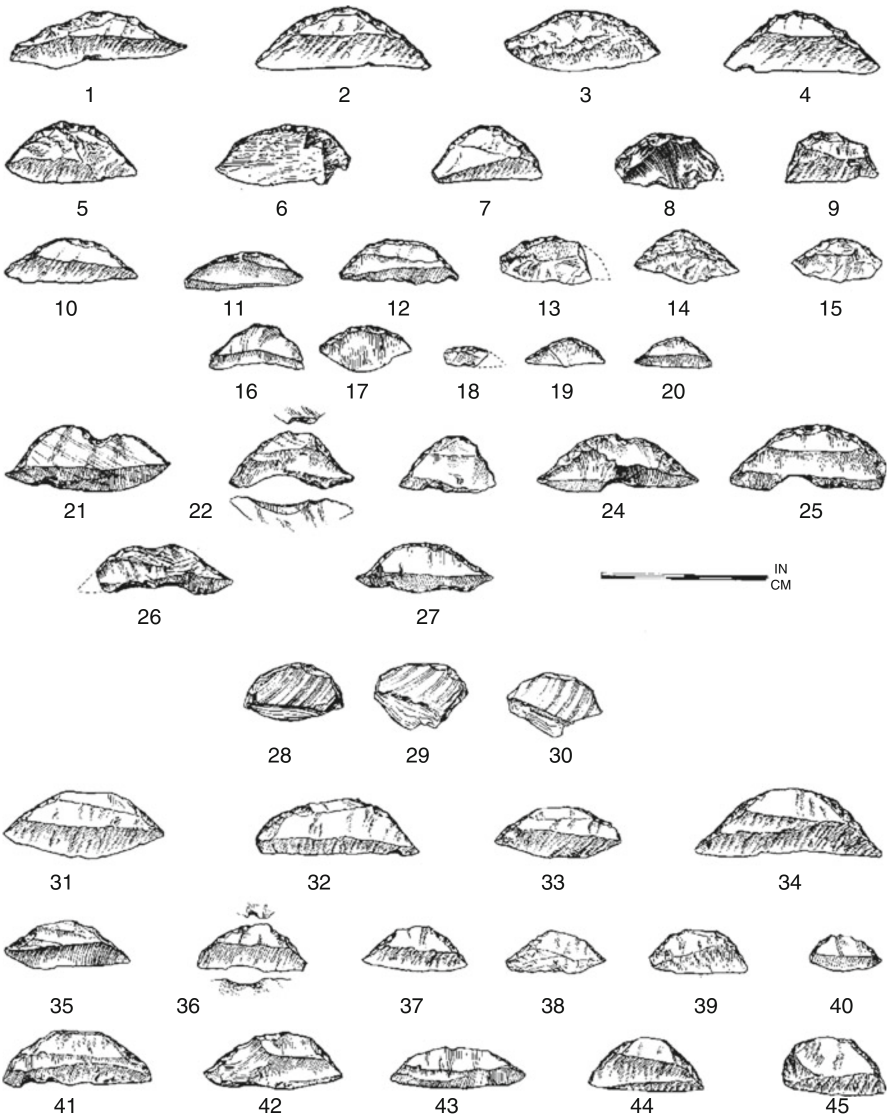


Fig. 2 Klasies River Mouth, South Africa. Highly standardized lithic artifacts from the Howiesons Poort assemblage ca. 75,000 years old (After Singer and Wymer 1982)

long argued for hafting based on patterns of damage to artifacts and use wear. Mastic attached to Middle Paleolithic artifacts at Umm el Tlel in central Syria also demonstrates the use of hafting and provides evidence for composite tools (Boëda et al. 1998). In Europe, a similar pattern is present with small-backed artifacts that almost certainly required hafting being recovered at (Conard 1992) Fig. 3 (Tönchesberg). European chipped stone points would have required hafting

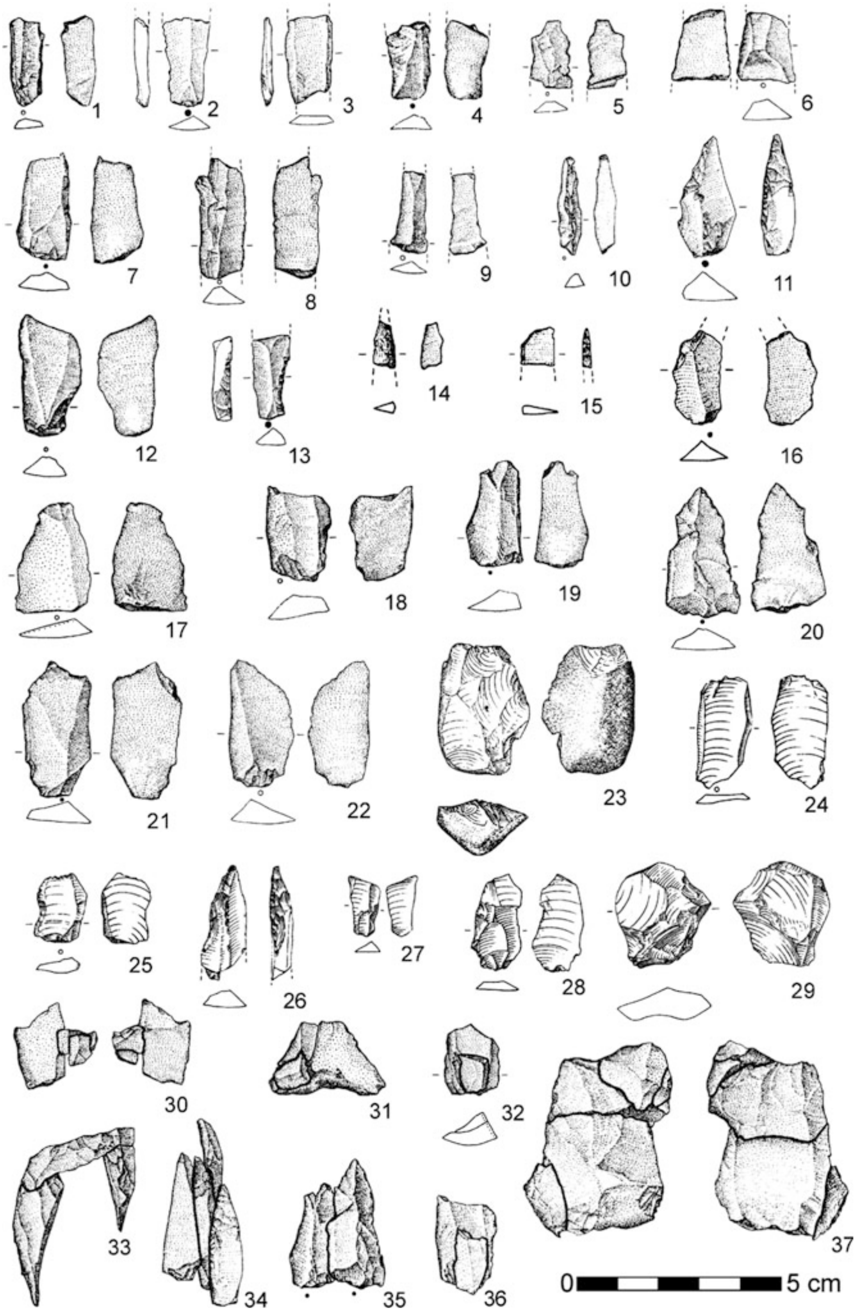


Fig. 3 Tönchesberg 2B, Germany. Middle Paleolithic assemblage with blades, bladelets, backed points, and backed bladelets and imported lithic materials ca. 100,000 years old (After Conard 1992)

as on other continents, and mastic has been recovered, for example, at the Middle Paleolithic sites of Königsaue (Mania and Toepfer 1973), Neumark-Nord (Mania et al. 1990; Meller 2003), Bocksteinschmiede (Wetzel and Bosinski 1969), and Inden-Altdorf (Pawlik and Thissen 2011) in Germany and Campitello Quarry in Italy (Mazza et al. 2006). The production of mastics such as birch pitch requires advanced knowledge of pyrotechnology and material sciences and provides good evidence for advanced cultural behavior (Wadley et al. 2009; Roebroeks and Villa 2010; Pawlik and Thissen 2011). Through experimental and use-wear studies, Rots has also demonstrated the hafting in multiple contexts during the Middle Paleolithic and MSA (Rots 2010, 2013; Rots et al. 2011).

Lithic assemblages of the MSA and Middle Paleolithic do not provide the evidence needed to define precisely when modern patterns of human behavior developed. They do, however, clearly show a heterogeneous pattern of technological development and transmission indicating that the beginnings of the LSA and Upper Paleolithic did not see fundamental revolutionary changes in technology across the Old World. This transition saw the further development of both new and older technologies. While more advanced forms of lithic technology came into broader use in the LSA and Upper Paleolithic, most of these technologies have well-documented precursors in earlier periods.

Organic Technology

The development of organic technology shows a pattern analogous to that of lithic technology. While the LSA and Upper Paleolithic are defined on the basis of new artifact forms that occur in easily detectable numbers, organic artifacts have antecedents extending into the ESA and Lower Paleolithic. Thus, the beginnings of the LSA and Upper Paleolithic reflect legitimate archaeological divisions, but the changes represent a further elaboration and intensification of technologies that in some cases existed earlier.

In regard to this question, the most important information comes from the finds from Schöningen in northern Germany, where Thieme's excavations have yielded eight wooden spears with multiple designs and other wooden tools dating to the late Lower Paleolithic about 300 Ka BP (Thieme 1997, 1999, 2007; Fig. 4). These tools are of the highest workmanship and lend support to the importance of wooden tools from Clacton-on-Sea (Oakley et al. 1977) and Lehringen (Thieme and Veil 1985). Middle Pleistocene hominins manufactured the spears and other wooden artifacts from Schöningen with great care, and their context demonstrates a high degree of planning depth, social organization, and sophisticated communication. Unless we postulate that this part of Northern Europe enjoyed a privileged position in human cultural evolution, we must conclude that organic technology and diverse well-made wooden tool assemblages were a part of the daily life of the Lower and presumably Middle Paleolithic inhabitants of Europe. These waterlogged sites provide a highly favorable setting for preservation that cannot be matched in other sedimentary settings, but occasional finds of preserved wood in Africa and

Fig. 4 Schöningen, Germany. Lower Paleolithic wooden spear and horse bones ca. 300,000 years old (Photo N.J. Conard)

the Near East leave room for optimism that future work may uncover comparable wooden artifacts.

Much has been made of the development and elaboration of bone, ivory, and antler tools in recent years (Gaudzinski 1999; d'Errico 2003; d'Errico et al. 2003; Soressi et al. 2013). MSA assemblages from sites including Apollo 11 (Vogelsang 1998), Klasies River (Singer and Wymer 1982) (see Fig. 5), Sibudu (Backwell et al. 2008), and Blombos (Henshilwood et al. 2001) have produced a wealth of bone artifacts (Fig. 4). Many examples are sharpened bones and bone splinters. Other bone tools show a series of notches or more enigmatic forms. An exceptional case is the elaborately made harpoons from Katanda in D. R. Congo (Brooks et al. 1995); these finds would be remarkable if they were indeed of early Late Pleistocene age. Certainly, by the middle of the Late Pleistocene, bone tools were widespread in the MSA.

The European Lower Paleolithic also documents early examples of bone tools including carefully manufactured hand axes (Segre and Ascenzi 1984; Gatti 1993).

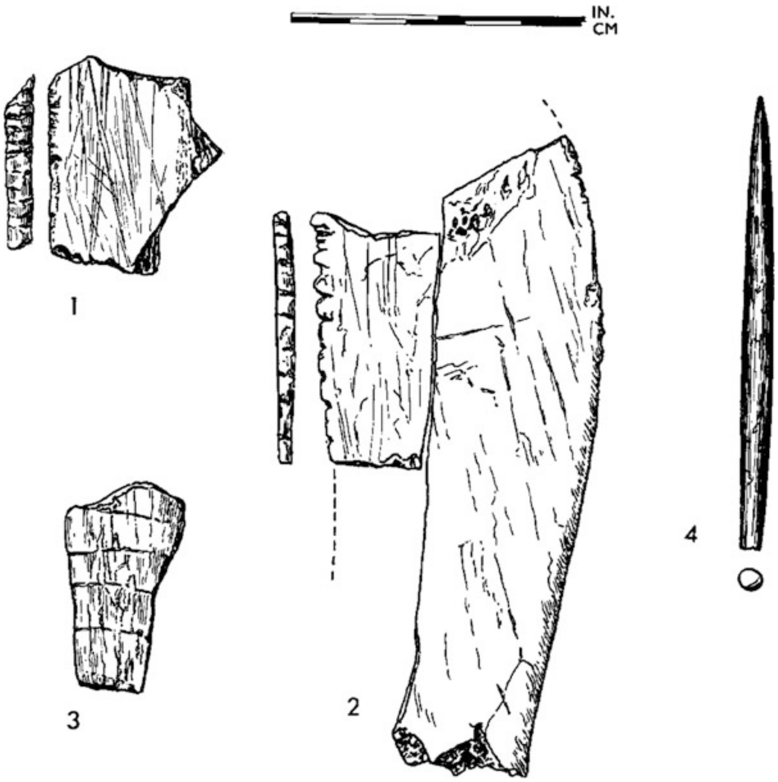


Fig. 5 Klasies River Mouth, South Africa. Bone artifacts from Middle Stone Age deposits ca. 75,000 years old (After Singer and Wymer 1982)

Similarly, bone tools are well documented at Middle Paleolithic sites, including Salzgitter-Lebenstedt (Gaudzinski 1999), Große Grotte (Wagner 1983), and Vogelherd (Riek 1934). Bone tools are by no means as common or complex as those of the Upper Paleolithic, but they no doubt existed in Middle Paleolithic assemblages. Bone tools were clearly used by late Neanderthals in many settings, and they have occasionally been documented in large numbers (d'Errico et al. 2003). While research continues to document more diverse and more specialized osseous tools associated with archaic hominins, such as those from Abri Peyrony and Pech de l'Azé I (Soressi et al. 2013), tools from the Middle Paleolithic are often less elaborate than the organic tools of the Upper Paleolithic. Split base points, for example, serve as diagnostic artifacts for the early Aurignacian over much of Europe and occur in significant numbers starting around 40 Ka (Albrecht et al. 1972; Hahn 1977).

Finally, the Late Pleistocene sees further evidence for cultural innovations that should be mentioned here. These innovations include the widespread use of grinding technology during the MSA and Middle Paleolithic of northern Africa (Wendorf et al. 1993; Van Peer et al. 2004), evidence for fire-making technology in the Swabian Aurignacian (Riek 1934, p. 161; Weiner and Floss 2004), and water transport technology in the form of perforated ostrich eggshells (Vogelsang 1998; Parkington et al. 2005; Texier et al. 2010; but see Kandel 2004). As these and other less well-studied categories of finds and behavioral innovations become topics of more systematic research, they will play a more prominent role in the discussions about the evolution of cultural modernity.

Subsistence

Patterns of subsistence vary in time and space due to changing environmental conditions and changes in technology combined with changing social and settlement strategies. Although most sites do not contain preserved botanical remains, there is every reason to assume that plants played an important part in the diet of all hominids, just as they do for all ethnographically documented societies (Owen 2005). The diet of Neanderthals as reflected in stable isotope data indicates a relatively high component of animal resources (Bocherens et al. 1999, 2001; Bocherens 2011), but these results do not preclude the use of plants in the diet, and even in the harshest arctic and desert environments, plants are seasonally available and nutritionally important.

This is not the place to summarize the history of research on this question, but recent decades have seen a shift from assuming that archaic and early modern humans practiced fully developed systems of hunting and food sharing, to a critical assessment and rejection of earlier interpretations by many Anglophone colleagues. More recently, many case studies have provided convincing evidence that both later archaic and anatomically modern humans practiced systematic hunting of large, medium, and small game. These data by no means suggest that patterns of subsistence are homogenous over whole continents or subcontinents, but the advocates of subsistence forms based on scavenging or ineffective forms of hunting (Binford 1989; Stiner 1990, 1994) seem to have overstated the case against the existence of reliable hunting economies within MSA and Middle Paleolithic societies (Marean and Kim 1998; Marean and Assefa 1999). In recent years faunal studies have increasingly shown a diverse array of adaptations among late archaic and early modern humans (Clark and Speth 2013), with increasing evidence for intensification and the exploitation of a broader range of taxa as hominin population densities increase and highly ranked faunal resources become less available (Stiner 2005, 2013; Speth 2010, 2013).

Again in this context, the finds from Schöningen are of central importance and have redefined the discourse on Lower Paleolithic subsistence. Thieme's (1997, 1999, 2007) team recovered eight spears from Schöningen in direct association with the bones of several dozen horses in deposits dating to ca. 300 Ka (Voormolen 2008; van Kolfschoten 2014). These discoveries from the mid-1990s brought the more extreme assessment of Lower and Middle Paleolithic subsistence based on obligate scavenging to an end, and as far as I am aware, the implications of these remarkable finds for documenting hunting of large game by archaic hominids and the implications of the recovery of a yew wood spear with the skeleton of an Eemian age forest elephant at Lehringen have not been questioned in recent years. These finds do not demonstrate that hunting large game was a universal phenomenon in the late Middle and Late Pleistocene, but they do document the existence of well-planned and successfully executed hunting of large and fast game using refined and deadly technology.

More mundane sources of information tend to support this view. Numerous faunal assemblages indicate that late archaic and early modern humans had frequent early access to game. In most settings, the possibility of scavenging cannot be completely excluded, but active hunting is the most parsimonious explanation for the faunal assemblages at sites including, for example, Salzgitter-Lebenstedt (Gaudzinski and Roebroeks 2000), Tönchesberg (Conard 1992), and Wallertheim (Schmidtgen and Wagner 1929; Gaudzinski 1995; Conard and Prindiville 2000). In other contexts, in many parts of Eurasia and Africa, similar evidence for the role of mammals in the diet of Middle Paleolithic and MSA people is available (Gaudzinski 1996; Marean and Kim 1998; Marean and Assefa 1999; Burke 2000; Bocherens et al. 1991, 2001; Costamagno et al. 2006; Rendu et al. 2011, 2012; Clark and Speth 2013). Finally, it must be stressed that scavenging fresh carcasses is an attractive economic option in contemporary hunting and gathering societies (O'Connell et al. 1988). Thus, there is no reason to stigmatize Paleolithic scavenging as a premodern adaptation.

In southern Africa, Klein and Parkington have developed new approaches and hypotheses for the development of subsistence practices during the MSA. Parkington (2001) stresses the key role of the exploitation of coastal resources for brain development and the origin of cultural modernity in coastal settings. He has also suggested that similar processes may have driven human evolution in other coastal environments, including the circum-Mediterranean region. Jeraldino and Marean (2010) have also emphasized the role of coastal adaptations in the later phases of human evolution in southern Africa. Klein (2009) has looked at small game such as tortoises and marine resources as playing an important role in MSA and LSA subsistence. He argues that until ca. 50 Ka, hunting was limited to comparatively easily hunted game and that people only started systematically hunting dangerous animals, including suids and buffalo in the late MSA and LSA. Klein sees this shift in subsistence as an indication of the rise of cultural modernity in connection with genetic mutations and the appearance of fully developed language. Both Parkington's and Klein's hypotheses have been received with considerable skepticism, but both hypotheses present entirely welcome, refutable models for the rise of cultural modernity. Given the general lack of clearly formulated models that provide causal explanations for the rise of behavioral modernity, these hypotheses, even if they are later demonstrated to be incorrect, have fostered considerable new research. This is certainly the case of the critical assessment of the early evidence for hunting by Binford and colleagues in the 1980s and 1990s.

Like the other data we have considered thus far, the evidence on subsistence during the Middle and Upper Pleistocene shows a pattern of advanced adaptations at an early date. With the possible exception of Parkington's model for increased use of marine resources in the Late Pleistocene, the data on subsistence tend to argue against a revolutionary change in economic and social behavior that defines the appearance of cultural modernity. The archaeological record of Mediterranean Europe demonstrates that Neanderthals also exploited marine resources as far back as during the late Middle Pleistocene and indicates that the early use of shellfish was not limited to modern humans living in Africa (Cortés-Sánchez et al. 2011). This being said, Stiner, Speth, and other scholars have documented how intensification led to the exploitation of lower ranked and more diverse resources as over the course of the Middle and Late Pleistocene (Stiner et al. 1999; Stiner 2005; Speth 2010, 2013; Steele and Klein 2009; Steele and Alverez-Fernandez. 2011; Conard et al. 2013). In general, hominins tend to exploit highly ranked resources when they are available, and thus, under similar conditions both archaic and modern hominins often exploited large- and medium-sized bovids, cervids, and equids when they were available (Münzel and Conard 2004).

Settlement

Reconstructing patterns of settlement and the organization of space is one of the more elusive ways of trying to define modern patterns of behavior. This relates to the general difficulty of reconstructing settlement dynamics in any period and particular problems associated with Paleolithic periods, where the amount and quality of data are generally poorer than in later periods. The analysis of Paleolithic settlement in the contexts of defining modern behavioral forms has two major approaches, one intrasite and the other regional.

Binford (1998), Wadley (2001), and others have argued that spatial organization within a find horizon can be used to define cultural modernity. Binford, for example, sees repetitive modular units of hearths and bedding areas in rock shelters as a hallmark of modern spatial organization. In his view, this pattern of spatial organization is not present before the LSA or Upper Paleolithic. Wadley sees a marked increase in spatial organization during the late MSA of Rose Cottage Cave in the Free State of South Africa as a further indication that the final stages of the MSA may reflect the period in which cultural modernity developed.

In Europe, Kolen (1999) has pointed to the lack of clear evidence for architecture as an indication that neither Lower nor Middle Paleolithic groups regularly built shelters as centers of social and economic interaction, as are known in many later archaeological periods. Instead, archaic humans used what Kolen refers to as "nests" to provide shelter. If correct, this would indicate that settlement dynamics of archaic humans, including Neanderthals, fell outside the range of culturally modern people. Several researchers have questioned this model and suggest that even if clear architectural features other than hearths are generally lacking before the Upper Paleolithic, late Middle Paleolithic sites document spatially structured activity areas similar to those one would expect in sites of modern hunters and gatherers (Vaquero et al. 2001, 2004; Conard 2001b; Chacón Navarro et al. 2012).

As with many of the criteria considered here, it is unclear to what extent taphonomic factors and the quality of data affect our interpretations. Kolen, however, is certainly correct to note that clear evidence for anthropogenic shelters and dwellings is extremely rare prior to the Upper Paleolithic. Although less effort has been invested in studying the spatial structure of MSA sites, recent work at Sibudu has demonstrated the use of bedding and regular site maintenance in multiple find horizons (Goldberg et al. 2009, 2013a; Wadley et al. 2011). This kind of research promises to provide insights into the organization of space by early modern humans in southern Africa.

At a larger scale of analysis, we see more tantalizing, yet largely inconclusive, evidence for the use of space and distant resources as indicators of behavioral modernity. Important works by Geneste (1988), Roebroeks et al. (1988), Floss (1994), and others examine the use of distant raw materials as a source of information on Paleolithic economic and spatial organization. Especially in the context of the continental European approaches to the study of patterns of lithic reduction and technology (Geneste 1988; Hahn 1988; Boëda et al. 1990), much research has been aimed at linking patterns of lithic technology to systems of mobility and settlement. These and other studies show the nearly universal pattern that more distant raw materials are present at sites in more reduced form than local raw materials. This applies for all Paleolithic periods. In later periods more raw materials from distant sources are transported to sites, but there is no specific moment that reflects a quantum shift from non-modern to modern patterns of behavior. Also, the “provisioning of place” (Kuhn 1995) – that is, the movement of quantities of raw material to sites for future use – is documented on sites of both modern and archaic hominins (Conard and Adler 1997).

Examination of the abundance of distant raw materials as a reflection of the size of territories and long-distance economic and social relationships has also provided ambiguous results. Middle Paleolithic assemblages document the use of raw materials from 100 or more km away (Floss 1994; Féblot-Augustins 1997). Nonetheless, such long-distance transport of tools and raw materials is still more common in the Upper Paleolithic, and the difference is more one of degree than of kind. So far these kinds of data have not led researchers to devise a reliable means of distinguishing between archaic and modern behavioral forms. These lithic data also suggest mosaic, context-dependent systems of adaptations with considerable variability, rather than a black-and-white world of unilinear evolution, in which quantum leaps between archaic and modern behavior can be readily identified.

Finally, an analysis of site types and links between sites within settlement systems shows considerable diversity in MSA and Middle Paleolithic systems of settlement, but no easily recognizable criterion for defining behavior modernity (Conard 2001c, 2004b). Here, as in other areas, I doubt whether the search for a holy grail of cultural modernity is a productive way of defining a research program. Scholars continue to struggle to identify the origins of a settlement system that reflects a symbolically mediated landscape inhabited by culturally modern people. Furthermore, if our definition of behavioral modernity includes all ethnographically documented patterns of settlement, we must concede that a nearly endless diversity of adaptations among subrecent hunters and gatherers are by definition modern and by no means easy to distinguish from hypothetical non-modern settlement dynamics as indicated by the distribution of archaeologically visible material cultural remains.

Beyond Technology, Subsistence, and Settlement

As the discussion above suggests, identifying clear criteria for behavioral modernity is probably more likely in the realms of ideology and symbolic communication than in the nuts and bolts archaeology of chipped stone and faunal remains. Here, I consider several lines of argument and sets of data that lie outside the pragmatic economic concerns of day-to-day subsistence.

Burials

Most of the more complete human skeletons from before the Middle Paleolithic and Middle Stone Age appear to be the result of extraordinarily favorable taphonomic contexts. Despite arguments to the contrary by Gargett (1989, 1999) and other colleagues, there are a wealth of Middle Paleolithic human skeletons that seem to have been buried deliberately (Solecki 1971; Trinkaus 1983; Defleur 1993). Such burials could be motivated by purely practical factors like the need to dispose of undesirable cadavers, but I think it is more likely that the numerous burials of Neanderthals and anatomically modern humans of the Middle Paleolithic reflect the deliberate burial of kin and are linked to personal and emotional ties between the living and the dead. Defleur (1993) has summarized much of the evidence for Middle Paleolithic burials and points to a number of convincing cases in Europe and the Levant. Debate on the presence of Middle Paleolithic burials continues with Rendu and colleagues (2013) favoring the existence of burials and Goldberg and colleagues (2013b) insisting on very high standards of data to document the presence of burials in the Paleolithic record. The question of the deliberate inclusion of grave goods and the identification of specific ritual practices is perhaps still more contentious and difficult to demonstrate beyond doubt.

In the Upper Paleolithic the data are unambiguous, and many burials preserve opulent grave goods that reflect the status of the individuals and the needs of the dead in the afterlife. Examples of burials from Sungir', Dolní Věstonice, the Grimaldi Caves, and other sites suggest that the system of beliefs in association with death and the afterlife were much more elaborate in Upper Paleolithic than Middle Paleolithic societies. These Upper Paleolithic burials are universally accepted as indicators of cultural modernity. As far as I am aware, aside from somewhat enigmatic cases like the highly fragmented and partially burnt assemblage from Klasies River Mouth in South Africa, the MSA and early LSA have not produced sufficient data for burials to allow conclusions to be drawn about practices and beliefs in sub-Saharan Africa. Human skeletal material, for example, in the Upper Cave of Zhoukoudian in China is suggestive of early Upper Paleolithic burials in the Far East (Pei 1939; Wang 2005), and the burials at Lake Mungo in Australia point to the cultural sophistication of the earliest inhabitants of that continent over 40 Ka BP (Thorne et al. 1999).

Pigments and Ground Ochre

In recent years, there have been a number of reports of early occurrences of pigments and discussions of the importance and meaning of the use of pigments (Barham 1998; McBrearty and Brooks 2000; d'Errico and Soressi 2002; Hovers et al. 2003; Dayet et al. 2013). On the basis of this work, it has become clear that pigments were used in some MSA contexts during the later Middle Pleistocene and in numerous MSA and Middle Paleolithic settings of the Late Pleistocene (Watts 1998). Southern Africa has yielded particularly abundant evidence for the use of ground ochre during the MSA. Barham's (1998) work at Twin Rivers in Zambia is a noteworthy example of the presence of many pieces of modified ochre in Middle Pleistocene contexts, and numerous MSA sites dating to the Late Pleistocene including Klasies River (Singer and Wymer 1982; d'Errico et al. 2012), Diepkloof (Dayet et al. 2013), Peers Cave, Hollow Rock Shelter (Watts 2002), Hoejiespunt (Will et al. 2013), Klipdrift (Henshilwood et al. 2014), Apollo 11 (Vogelsang 1998), and Blombos (Henshilwood et al. 2001) have produced much evidence for grinding of pigments. Recent work at Blombos has documented tool kits for making and storing pigments (d'Errico and Stringer 2011). Parkington has argued that the use of pigments provides additional indications of the advent of behavioral modernity in the MSA, particularly in more coastal settings, where Howiesons Poort and Still Bay assemblages are concentrated. Watts (1998, 2002) has reviewed the evidence for the use of pigments in the MSA and concludes that they are extremely common at many MSA sites and reflect a widespread ability to structure the world into a symbolically organized whole. Watts rejects the hypothesis that ground ochre was primarily used for strictly utilitarian purposes, including tanning hides, while Wadley (2005; Wadley et al. 2009) emphasizes the practical uses of ground ochre. Through a program of experimental and archaeological observations, Wadley has shown that worked ochre from Sibudu, and likely elsewhere, often served as a component of mastic.

In the Levant and Europe, Hovers et al. (2003) see strong evidence for the use of ochre at Middle Paleolithic sites including Qafzeh (Vandermeersch 1969). Sites including Maastricht-Belvédère (Roebroeks et al. 2012), Pech de l'Azé (Bordes 1972; d'Errico and Soressi 2002), Cueva de los Aviones, and Cueva Antón (Zilhão et al. 2010) document the use of red, yellow, and black pigments in Middle Paleolithic contexts and suggest that Neanderthals regularly used pigments. Zilhão and d'Errico emphasize that the use of symbols and complex technology evolved independently among Neanderthals and was not the product of acculturation after contact with fully modern humans as has been argued by White (2000), Hublin et al. (2013), and Mellars (2005). The potential uses of ground ochre include body painting, rock painting, drawing, ritual, medicinal, as well as more mundane purposes. Although we rarely have reliable information on the specific use of these early occurrences of ochre, they are presumably, at least in some settings, such as in Middle Paleolithic burials, connected with religious beliefs that speak for a high level of cultural development and a significant degree of symbolic communication (Hovers et al. 2003). As with other potential indicators of advanced cultural attributes discussed above, the use of ochre does not appear to reflect a quantum leap signifying the shift from archaic to modern patterns of behavior. Both anatomically modern and archaic humans used pigments and presumably attached symbolic meaning to red, black, and perhaps other ground mineral pigments. Here, however, Wadley's caveats against assuming that ground ochre served as primarily as pigment should be reiterated. Given the likely use of mineral pigments in the MSA and Middle Paleolithic, the use of organic pigments is likely, even if difficult to demonstrate with direct archaeological observations.

Decorated Objects and Nonfigurative Representation

There is a long history of claims for deliberate nonutilitarian modification of objects in Paleolithic contexts. These include finds from the Lower Paleolithic, such as incised bones from Bilzingsleben (Mania 1990; Steguweit 2003), and many finds from later periods. These objects are often controversial and are usually not accepted as demonstrating complex symbolic communication. Following other lines of argument, colleagues have suggested that the perfect symmetry of some hand axes indicates an advanced aesthetic development, but Wynn (1995) and Haidle (2004) argue that hand axes do not necessarily reflect symbolically based communication or language. Over the course of the Middle Paleolithic and MSA, larger numbers of enigmatic objects have been published, including the cross-incised stone and modified fragment of a mammoth tooth from Tata, Hungary (Vértes 1964), and the so-called mask from La Roche-Cotard (Lorblanchet 1999). Some researchers have included evidence for collected fossils or curated natural products as indicators of advanced aesthetic and behavioral patterns (Schäfer 1996).

Particularly in recent years, the MSA has produced a number of incised objects that have been taken as evidence for symbolic communication and a high degree of cultural development. Important examples of these finds include engraved linear and crosshatched patterns on pieces of ochre from Still Bay deposits at Blombos dating to ca. 75 Ka (Henshilwood et al. 2002) and incised pieces of ochre from, for example, Peers Cave, Klein Kliphuis (Mackay and Welz. 2008), and Klasies River Cave 1 d'Errico et al. (2012). Current excavations at Diepkloof have produced hundreds of fragments of decorated ostrich eggshells from Howiesons Poort contexts including pieces that are interpreted as originating from decorated ostrich eggshell flasks (Parkington et al. 2005; Texier et al. 2010). Similar finds have also been recovered from MSA contexts at sites including Klipdrift (Henshilwood et al. 2014) and Apollo 11 (Vogelsang 1998). These finds are unquestionably the result of deliberate manufacture and probably reflect the desire of the craftsperson to convey symbolic content and aesthetically meaningful as well as practical information to members of his or her social group. There can be little doubt that such carefully produced decorated objects and the nonfigurative representations they carry communicated specific information from the maker to people who used or saw these objects. Deciphering the specific meaning broadcast through these finds is not easy, and few specific explanations for their meaning have been presented. With increasing amounts of carefully executed fieldwork during the MSA, there is reason for optimism that contextual information will help archaeologists to develop hypotheses to explain the meaning of these finds. The concentration of these finds in southern Africa may be simply a reflection of the intensity of high-quality research in this region, or perhaps an indication that this form of storing and using symbolic information was more common in this part of the world than in other geographic areas. Some colleagues accept these finds as definitive evidence of cultural modernity with fully developed symbolic communication, modern cognitive abilities including language (Henshilwood et al. 2002; d'Errico et al. 2003; Texier et al. 2010). The wealth of finds of engraved objects in the southern African MSA demonstrate that symbolic artifacts of this kind are not as exceptional as initially thought and that marked and decorated objects have a prominent role in the symbolic repertoire of MSA material culture.

Personal Ornaments and Jewelry

The manufacture and use of personal ornaments convey social information about individual identity and group affiliation. This means of projecting assertive individual style or emblematic style reflecting social affiliation within a larger demographic group (Wiessner 1983) is an important characteristic of modern behavioral patterns and has been the focus of much recent research (Vanhaeren 2002; Kölbl and Conard 2003; Vanhaeren and d'Errico 2006). The archaeological distribution of ornaments provides a clearer signal than many of the classes of information considered above.

Early evidence for the use of marine shells as ornaments comes from burial contexts from Qafzeh Cave in Israel and dates to about 100 Ka (Bar-Yosef and Vandermeersch 1993). Perforated marine shells of similar age are also documented at Skhūl Cave in Israel (Vanhaeran et al. 2006) and Grotte des Pigeons in Morocco (Bouzouggara et al. 2007). Slightly younger examples of perforated marine shell ornaments come from Still Bay deposits at Blombos Cave dating to about 75 Ka (Henshilwood et al. 2004, 2011) and MSA contexts at Sibudu (d'Errico et al. 2008). Starting roughly 40 Ka, personal ornaments have been documented in many parts of the Old World from multiple regions of Africa, Eurasia, and Australia. Early ornaments include ostrich eggshell beads from early LSA contexts in Enkapune Ya Muto rock shelter, Kenya, with associated radiocarbon measurements between 30 and 40 Ka (Ambrose 1998). AMS radiocarbon dates directly on ostrich eggshell beads from deposits representing the transition from the MSA to LSA at Mumba Cave in Tanzania (Fig. 6; Weiß 2000; Conard 2004a) have yielded multiple dates

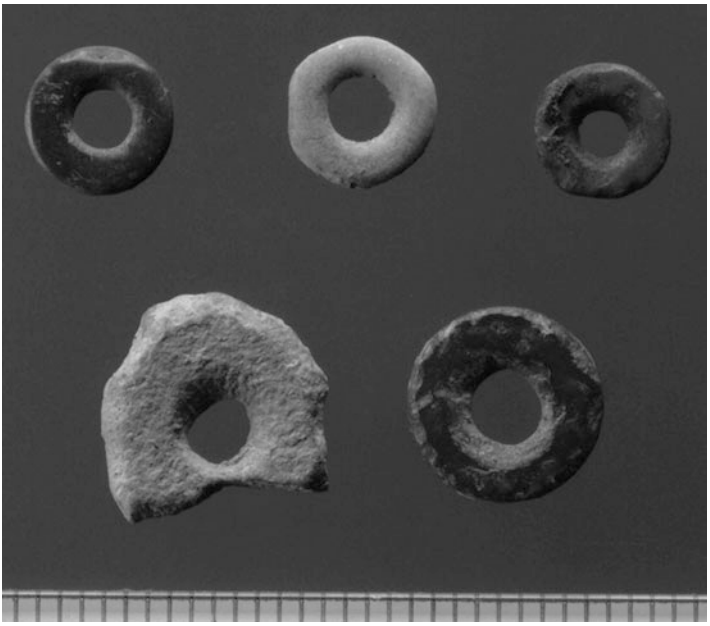


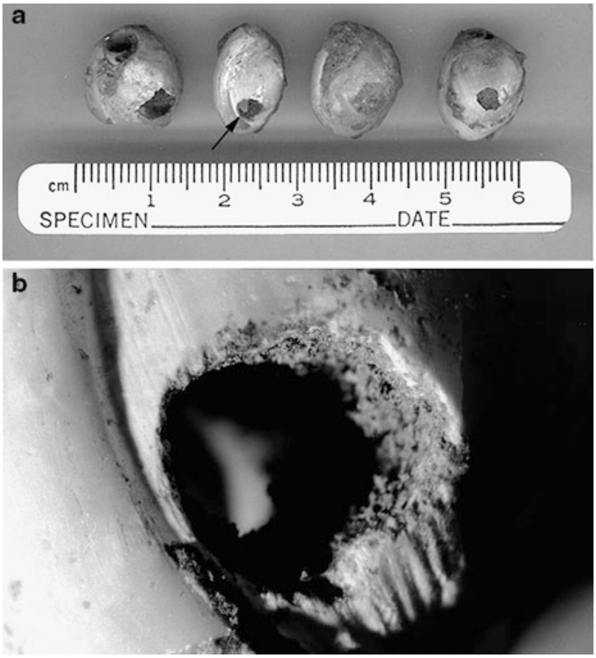
Fig. 6 Mumba Cave, Tanzania. Ostrich eggshell beads radiocarbon dated between 29,000 and 33,000 radiocarbon years ago scale in millimeters (Photo H. Jensen)

between 29 and 33 Ka uncalibrated radiocarbon years, or starting roughly 36 Ka cal BP, and lend support to the early dates from Enkapune Ya Muto. There is every reason to assume that these East African ornaments were made by anatomically and presumably culturally modern people.

Excavations at Ksar Akil in Lebanon (Azoury 1986) and at Üçagizli in the Hatay Province of Turkey (Kuhn et al. 1999, 2001) have produced rich assemblages of perforated marine shells from Initial Upper Paleolithic contexts dating to about 40 Ka (Fig. 7). Similar finds have been recovered from other Mediterranean early Upper Paleolithic contexts, including Riparo Mochi on the Ligurian Coast of Italy (Kuhn and Stiner 1998; Stiner 1999). Douka (2013) has recently developed new methods for dating marine shells and has repeatedly demonstrated the finds date to roughly 40 Ka BP. With the exceptions of late Middle Paleolithic sites of Cueva de los Aviones and Cueva Antón in Spain (Zilhão et al. 2010), the perforated shells have normally been interpreted as having been produced and used by anatomically modern humans.

In Europe there is considerable evidence for a rapid spread in the use of ornaments with the beginning of the Upper Paleolithic. In addition to the Spanish examples, Neanderthals apparently created a wide range of perforated and incised ornaments in Châtelperronian contexts such as at Grotte du Renne at Arcy-sur-Cure (Leroi-Gourhan and Leroi-Gourhan 1964; d'Errico et al. 1998; Baffier 1999). These finds remain at the center of considerable debate about whether or not Neanderthals developed advanced symbolic communication. At more or less the same time,

Fig. 7 Üçagizli Cave, Turkey. Perforated marine shell ornaments dating to ca. 40,000 radiocarbon years ago (After Kuhn et al. 2001)



numerous examples of early Aurignacian ornaments have been recovered from several regions including the Swabian sites such as Vogelherd, Geißenklösterle, and Hohle Fels (Conard 2003a; Higham et al. 2012; Wolf et al. 2013; Fig. 7). In addition to incised and perforated natural forms such as teeth, these artifacts include diverse ornaments made of mammoth ivory. It is noteworthy that many of the oldest forms of ornaments in Europe are not only perforated natural objects but also completely carved, three-dimensional ivory beads, pendants, and figurines in which the maker completely dictated the form of the artifact (Conard 2008, 2010).

Although earlier examples of personal ornament are known, by around 40 Ka ornaments are well documented across much of the Old World. These data are consistent with the hypothesis that modern cultural behavior spread rapidly between roughly 30 and 50 Ka. Personal ornaments from the Upper Cave of Zhoukoudian, Shuidonggou Locality 2 (Gao et al. 2002), and Xiaogushan Cave (Archaeological Institute of Liaoning Province 2009) document the presence of this class of artifacts in association with flake-based lithic assemblages in northeastern China by 30 Ka (Pei 1939; Conard 2013). Shell beads from Mandu Mandu Creek Rock Shelter in Western Australia dating to more than 30 Ka (Morse 1993) suggest that the use of personal ornaments was indeed widespread at an early date. Although Australia lies outside the scope of this review, the colonization of Sahul was an event in prehistory that required crossing the vast open water of Wallacea with rafts or other forms of boats. The best available dates for the colonization lie in the range of ca. 42–45 Ka and fit with the pattern suggesting the rapid spread of advanced behavioral patterns at about this time (O'Connell and Allen 1998, 2004).

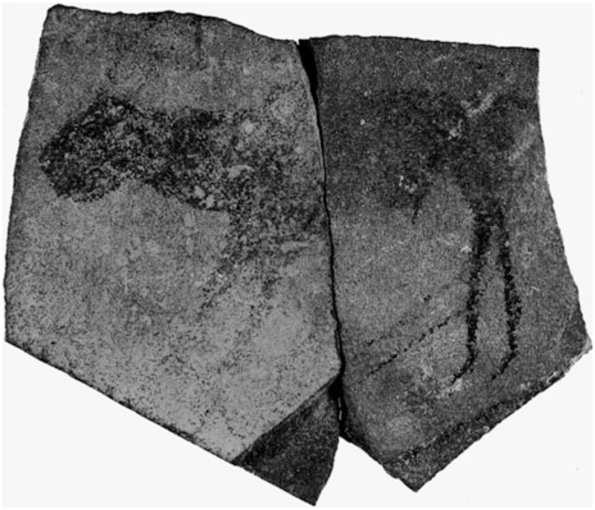


Fig. 8 Apollo 11 Cave, Namibia. Figurative painting from Middle Stone Age deposits dated with radiocarbon to ca. 27,000 years old (After Vogelsang 1998)

Figurative Representations

The presence of figurative art is universally accepted as an indication of behavioral modernity. As far as I am aware, no one has disputed that figurative representations are a hallmark of modern cultural behavior. Mann (2003) has gone so far as to argue that representational art is the "gold standard" by which behavioral modernity can be identified and measured. This being said, figurative representations can be viewed as documenting fully developed symbolic communication, but the lack of such artifacts in the archaeological record tells us little since many recent archaeological cultures lack figurative art. Clearly many forms of symbolic communication, including speech, stories, and song, are archaeologically nearly invisible.

In Africa, the earliest figurative art is from the late MSA of Apollo 11 (Fig. 8), dating between 25,500 and 27,500 radiocarbon years ago (Vogelsang 1998). These examples of painted mobile art depict a number of animals, geometric forms, and a therianthrope. The Middle Pleistocene-aged, anthropomorphic-shaped stone from Tan-Tan, Morocco (Bednarik 2003), much like a similar object from Berekhat Ram, Israel (Goren-Inbar 1986; Goren-Inbar and Peltz 1995; d'Errico and Nowell 2000), appears to be a modified natural form rather than deliberately carved figurine. In the Levant there is little or no evidence of figurative art before 30 Ka.

The situation in Europe is very different, in that several sites have provided evidence of figurative representation between 30 and 40 Ka. The earliest figurative art includes the mammoth ivory figurines from four caves in Swabia in southwestern Germany (Hahn 1986; Schmid 1989; Conard and Bolus 2003; Conard 2003b; Conard 2009; Conard et al. 2009a) and several red monochrome paintings from Fumane in northern Italy (Broglio 2002; Broglio and Dalmeri 2005). The Swabian caves of Vogelherd, Hohlenstein-Stadel, Geißenklösterle, and Hohle Fels (Fig. 9a, b)

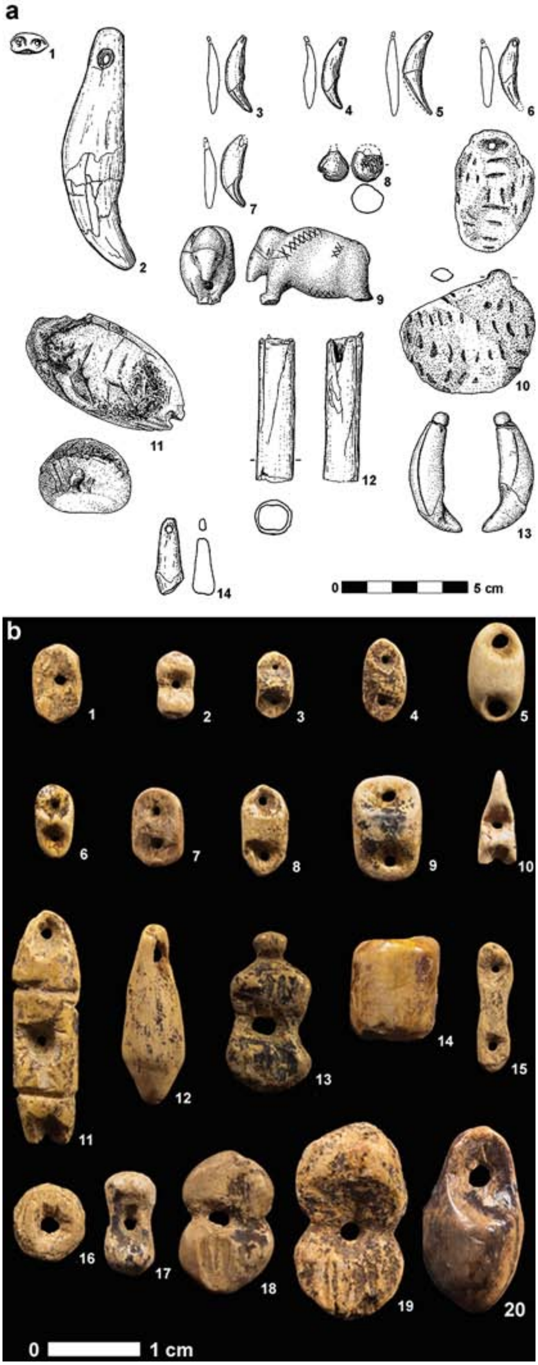


Fig. 9 (**a**) Sirgenstein, Bockstein Cave, Hohlenstein-Stadel, Vogelherd, Bockstein-Törle, Germany. Personal ornaments from the Aurignacian dating to ca. 36,000–30,000 radiocarbon years ago (After Conard 2003a) (**b**) Ivory ornaments from the Swabian Aurignacian, ca. 34 Ka radiocarbon years BP. *1–5* and *11–16* Hohle Fels; *6–10* and *17–20* Vogelherd (Photo: W. Binczik; Eberhard Karls Universität Tübingen)

Fig. 10 Mammoth from Vogelherd, ca. 34 Ka radiocarbon years BP (Photo: H. Jensen; Eberhard Karls Universität Tübingen)

have produced about 50 mostly fragmentary, small, ivory figurines and isolated representations in bone and stone dating well in excess of 30,000 radiocarbon years, which corresponds to closer to 40 Ka in calendar years. Due to the noisy radiocarbon signal in this period and above-average ^{14}C production, the radiocarbon ages at the Swabian caves and the similarly aged deposits from Fumane significantly underestimate the age of these artworks (Conard and Bolus 2003). The most recent calibrated radiocarbon dates place the beginning of the Swabian Aurignacian at about 42.5 Ka and at the very beginning of this cultural tradition (Higham et al. 2012). The Swabian ivory figurines include depictions of lions, mammoths (see Fig. 10), horses, bisons, bears, a water bird, a fish, numerous unidentified fragments, and three therianthropes that combine features of lions and humans (Hahn 1986; Conard 2003b; Wehrberger 2013; see Fig. 11). The depictions of mythical imagery, in the form of therianthropic representations, appear simultaneously with other more naturalistic depictions of animals and humans and provide unique insight into the system of beliefs of Paleolithic peoples (Conard 2010). These artworks from the Swabian caves are usually small and beautifully carved. The oldest of the figurines is likely a remarkable female figurine, the "Venus of Hohle Fels" (Fig. 12) that excavators found in the basal Aurignacian deposit of Hohle Fels Cave in the Ach Valley (Conard 2009). This find, and abundant ivory working debris from the basal Aurignacian at Hohle Fels and the lower Aurignacian at Geißenklösterle, demonstrates that this rich tradition of ivory carving in the region dates back to the start of the Aurignacian, the period in which modern humans initially migrated up the Danube corridor. The early figurative depictions from Swabia suggest that figurative representations evolved very quickly and reached a high level of refinement almost immediately. These finds stand in sharp stylistic contrast to the highly schematic paintings of animals, unknown forms, and a possible therianthrope from Fumane (Broglio 2002).

Fig. 11 *1* Geißenklösterle, *2* Hohle Fels, *3* Hohlenstein-Stadel, Germany. Three lionmen carved from mammoth ivory, ca. 34,000 radiocarbon years BP (Photo: *1* P. Frankenstein, H. Zwietasch; Landesmuseum Württemberg, Stuttgart. *2* H. Jensen; Eberhard Karls Universität Tübingen. *3* Y. Mühleis; Landesamt für Denkmalpflege im RP Stuttgart)

Geißenklösterle has also produced a painted rock from this period that preserves traces of red, yellow, and black pigments (Hahn 1986).

Most of the spectacular paintings from Grotte Chauvet in the Ardèche region of southern France (Fig. 13) appear to postdate the examples of figurative art from Swabia and Fumane (Clottes 2001). Here, numerous depictions of animals date back as far as 32,000 radiocarbon years ago, which corresponds to roughly 36 Ka cal. The selection of animals depicted in Chauvet, with an emphasis on dangerous, strong, and large animals, shows remarkable similarities to the Aurignacian figurines from Swabia and no stylistic similarities to the schematic depictions from Fumane. Therianthropic representations are present at these sites and, as in Swabia and at Apollo 11, suggest that depictions of mythical images have been part of the cultural repertoire of many groups of people from the beginning of artistic representation. Other important sites in this context include Stratzing in Lower Austria,

Fig. 12 Hohle Fels, Germany. Female figurine carved from mammoth ivory, age ca. 36 Ka radiocarbon years BP (Photo: H. Jensen; Eberhard Karls Universität Tübingen)

Fig. 13 Grotte Chauvet, France. Early Upper Paleolithic parietal art radiocarbon dated to ca. 30,000 years ago (After Clottes 2001)

where a human figurine of stone has been dated to between 30 and 32 Ka (Neugebauer-Maresch 1989). Abri Cellier, La Ferrassie, Abri Blanchard, and Abri Castanet in southwestern France have produced an impressive group of engraved representations in stone of animals and vulvas dating between ca. 30 and 34 Ka radiocarbon years ago (Leroi-Gourhan 1995; White et al. 2012). Recently paintings in Peștera Coliboaia, Romania, have been discovered dating to ca. 32 Ka that show stylistic similarities to the paintings in Grotte Chauvet and suggest that Chauvet may not stand entirely alone with respect to early parietal art (Besesek et al. 2010; Clottes et al. 2011).

These figurative depictions from European contexts are the oldest known worldwide. They all date to the early Upper Paleolithic and were presumably made by modern humans; however, as far as we can tell, Neanderthals still occupied parts of Europe at this time, roughly 40 Ka. At present, there is no concrete evidence for a direct association between modern humans and early figurative art in Swabia. Thus, the hypothesis that Neanderthals created the figurative art and other remarkable finds of the early Aurignacian, although highly improbable, had not been entirely refuted (Conard et al. 2004a).

The specific context in which figurative art developed has been the subject of considerable discussion of late and will not be elaborated on here (Lewis-Williams 2002; Conard and Bolus 2003). Regardless of the specific social-cultural conditions that led to the development and spread of figurative art, there is a broad consensus among archaeologists and paleoanthropologists that the makers of these early artistic traditions were culturally modern people (Churchill and Smith 2001; Klein 2009). While many other advanced behavioral forms have precursors in earlier periods, there is no convincing evidence for figurative depictions prior to the beginnings of the European Upper Paleolithic.

Music

Perhaps because of the long research tradition and favorable taphonomic conditions, the earliest examples of musical instruments have been recovered from early Aurignacian contexts in Swabia (Hahn and Münzel 1995; d'Errico et al. 2003; Conard et al. 2004b, 2009b). As with figurative representations, evidence for music and musical instruments can be seen as an indication of fully developed cultural forms based on symbolic communication. The assumption in this context is that where there is figurative art and music, there must have been fully developed language, by which Paleolithic people assigned specific concrete and abstract meaning to words and could efficiently communicate information about the past, present, and future. Thus, where there is figurative art and music, there must have been behaviorally modern people.

While speech, song, music, and dance presumably existed still earlier, the oldest musical instruments known are two bone flutes from swan radii and one mammoth ivory flute from the Aurignacian archaeological horizon II at Geißenklösterle (Hahn and Münzel 1995; Conard et al. 2004b), fragments of a bone and ivory flute from Vogelherd (Conard and Malina 2006), and fragments of two ivory flutes and one nearly complete flute carved from the radius of a griffon vulture from the basal Aurignacian of Hohle Fels (Conard et al. 2009b; Fig. 14). These deposits have been dated by thermoluminescence and radiocarbon to about 40–37 Ka. Reconstructions

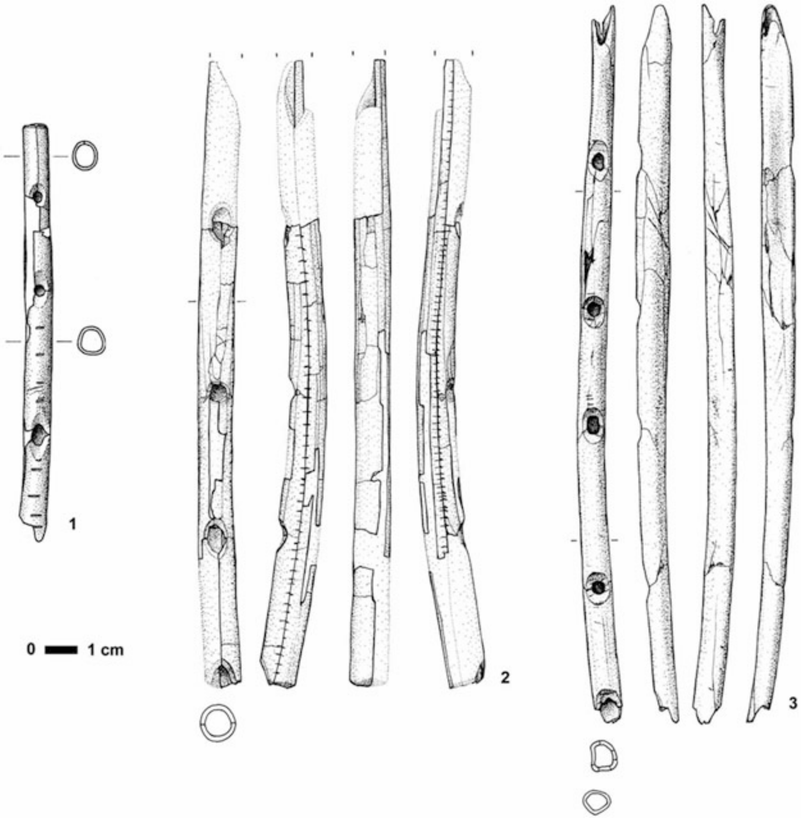


Fig. 14 *1* Geißenklösterle Flute 1 from a swan radius, *2* Geißenklösterle Flute 3 from mammoth ivory, and *3* Hohle Fels Flute 1 from a radius of a griffon vulture (Drawing: *1* A. Frey. *2–3* R. Ehmann. Eberhard Karls Universität Tübingen)

of the swan bone flutes produce a high-pitched but pleasing music. Friedrich Seeberger (2002, 2004) has recorded a CD of Ice Age music played on a reconstructed bone flute of the kind known from Geißenklösterle. This flute can be played without a reed and is clearly a flute rather than a trumpet-voiced instrument as suggested by d'Errico and colleagues (2003). The ivory flutes and the griffon vulture flutes can be played in similar manners and produce attractive tones and musical possibilities but have a lower register of tones due to their larger diameters. While Aurignacian musicians may have played very different-sounding music, Seeberger's playing provides a striking impression of what this early Upper Paleolithic music may have sounded like. Interestingly, all of the flutes and fragments of flutes recovered thus far are from horizons containing a wide range of rich settlement debris from day-to-day life, suggesting that bone and ivory flutes and the music played on them formed part of the daily lives of the Aurignacian inhabitants of the Swabian Jura. Finally, it is no coincidence that all of these early flutes have been found in caves. The Aurignacian musicians of the region certainly chose to use the outstanding acoustic characteristics of the caves to accentuate the impact of their music.

Other sites, most notably Isturitz in the French Pyrenees, have produced additional flutes and indicate that wind instruments were in fairly wide use during the early Upper Paleolithic (Buisson 1990; d'Errico et al. 2003). Of course, there are countless other less conspicuous forms of percussion and wind instruments that could have existed during the early Upper Paleolithic or still earlier, yet they remain to be identified. Claims for earlier examples of Middle Paleolithic flutes have generally been met with skepticism in archaeological circles, as was the case with recent claims for a Middle Paleolithic flute made from a cave bear bone from Divje Babe in Slovenia (Turk 1997; Albrecht et al. 1998).

Conclusions

This overview has touched on some, but by no means all, of the evidence for the development of behavioral modernity. I have mentioned some of the main data sets and lines of reasoning that play a role in the discussions and debates about the origins of modern behavior. This leads to the question of by what means, where, and under what circumstances behavioral modernity arose and which of the hypotheses for its origins lies closest to the mark?

The answers to these questions depend on how the evidence is weighed and interpreted. From my point of view, there can be no doubt that European Aurignacian societies by roughly 40 Ka had all of the hallmarks of modern behavior including Mann's "gold standard" of figurative art as well as musical instruments. The best evidence for early figurative art and music comes from the caves of the Swabian Jura. While one could argue that some important Upper Paleolithic artifact forms developed in the Upper Danube drainage in the period around the time of the arrival of modern humans, naming this region as the single global center for the origin of cultural modernity would be a radical and naive interpretation. The broadly contemporary finds of figurative art from Fumane, and slightly later finds from southern France and the Wachau of Austria, indicate that the beginnings of the Upper Paleolithic reflect a time in which earlier behavioral forms were replaced by behavioral forms that lie within the range of modern variability. This transition appears to have begun across much of Europe about 45 Ka when modern humans entered a continent inhabited by Neanderthals. Based on the presence of late Neanderthals in several regions of Europe (Hublin et al. 1995; Smith et al. 1999), it appears that there must have been a period in which both archaic and modern humans coexisted in Europe, and contact between the two forms of people must have occurred (Conard 2006). Given the poor chronostratigraphic resolution and scarcity of human fossil material during this key period between roughly 30 and 45 Ka, it is difficult to specify exactly how long both hominins coexisted in specific regions, but progress is being made on clarifying the regional sequences and the most recent estimates suggest a coexistence of several thousand years (Higham et al. 2011, 2012, 2014).

Early anatomically modern humans at Skhūl and Qafzeh in the Levant predate many remains of Neanderthals in southwestern Asia and point to an initially successful colonization of the region. The reappearance of Neanderthals in the Levant by roughly 60 Ka suggests that Neanderthals had more successful adaptations and demographic advantages over anatomically modern humans in interactions dating to the middle part of the Late Pleistocene. While evidence for strict contemporaneity is still lacking, this observation indicates that in some settings in which both hominins produced Middle Paleolithic artifact assemblages, Neanderthals had the upper hand (Conard 2008). However, in later encounters the situation was different. At about 45 Ka, modern humans arrived in western Eurasia with more developed cognitive skills (Lewis-Williams 2002) or behavioral advantages (Marean 2005) that led to demographic success relative to the indigenous Neanderthals. In western Eurasia, a period of dynamic equilibrium between Neanderthals and anatomically modern populations existed, in which moderns presumably profited from the knowledge and cultural practices of the "archaics" and vice versa.

There is little reason to postulate a violent rapid advance of Neanderthals into the Levant replacing indigenous anatomically modern humans in the middle of the Late Pleistocene, and similarly there is little reason to assume that the arrival and spread of modern humans into Europe was either universally rapid or brutal. On the contrary, the transition from the Middle to the Upper Paleolithic and the infiltration and eventual complete dominance of *Homo sapiens sapiens* in Eurasia probably took on countless local ecologically and historically dictated variants in which there was give and take between archaic and modern humans. This pattern is reflected in the diverse regional signatures of the archaeological records from nearly every region that has produced relevant data for this transition. These data show very different archaeological signatures depending on the environmental and social-cultural setting encountered by incoming populations (Conard 1998; Conard and Bolus 2003). Evidence from the sites occupied by late Neanderthals indicates that they too manufactured and used ornaments (Baffier 1999), and as we have seen above, there is little that separated the patterns of technology, subsistence, and settlement reflected in Middle Paleolithic artifact assemblages from those of the MSA or early Upper Paleolithic. Still, some time presumably in the early and middle parts of the Late Pleistocene and certainly no later than 40 Ka, people began producing material cultural remains that allow us to identify behavioral modernity. This pattern of behavior was carried primarily, but perhaps not exclusively, by anatomically modern humans (Zilhão et al. 2010; d'Errico 2003).

Many characteristics of modern behavior can be found across much of the Old World, and the distribution of advanced cultural traits is significantly determined by the intensity of research in different regions. The recent trend of important discoveries being made in MSA contexts in southern Africa will no doubt continue as more work is done. The data from Klasies River, Apollo 11, Rose Cottage Cave, Blombos, Sibudu, Diepkloof, the Pinnacle Point sites, and Klipdrift clearly show the enormous potential of the subcontinent. Elsewhere, a similar intensification of research would perhaps produce a similar increase in data relevant to the definition of cultural modernity. Although this chapter has not addressed these regions in detail, research in China and East Asia is improving the database and documenting new patterns of cultural evolution during the Late Pleistocene (Wang 2005; Conard 2013; Ono 2013). Western Eurasia also has considerable potential, but there is less reason to assume that the archaeological record will be so radically transformed by further work. Instead, important gaps will be filled and gradually a more complete picture of the highly variable behavioral patterns during the Lower, Middle, and Upper Paleolithic will emerge. With time we will be better able to develop and test new hypotheses for the evolution and spread of cultural modernity, and this problematic concept will continue to undergo debate (Henshilwood and Marean 2003; d'Errico and Stringer 2011). For example, colleagues including Shea (2011) have long argued that we should jettison the simplistic and controversial concept of behavioral modernity and instead work to gain a better understanding of behavioral variability. Researchers in Tübingen are developing a model for behavioral plasticity and the evolution of "hyperplasticity" to help explain how cultural complexity developed over the course of human evolution (Kandel et al. 2014). This model arises in part from the observation that, over the course of human evolution, behavioral patterns become increasingly detached from direct environmental causality, and ever more behavioral patterns and solutions to problems appear in the archaeological record. Hominins increasingly have created their own environment until they could occupy even the most inhospitable parts of the planet. This pattern continues today, and the concept of hyperplasticity offers the advantage of not reducing human evolution to a dichotomy between archaic or modern behavior.

Based on the data presented above, a strict unilinear and monocentric model for the evolution of behavioral modernity appears less likely than a pattern of *mosaic polycentric modernity* (Conard 2008, 2010). These data suggest that MSA and Middle Paleolithic societies generally existed within regionally specialized social groups with highly variable material culture. Whether anatomically modern or archaic, these people lived at a similar level of technological and cultural development. Perhaps by the early part of the Late Pleistocene or possibly as late as 40–50 Ka, full behavioral modernity developed in Africa and in Eurasia. Most archaic humans appear not to have mastered the repertoire of new behaviors including fully developed symbolic communication. If, however, some late archaic humans, including Neanderthals, were culturally fully modern as d'Errico and Zilhão have long argued, their behavioral patterns still put them at a reproductive and demographic disadvantage in comparison with the anatomically and culturally modern social groups that propagated across the Old World. The extinction of Neanderthals and Denisovans (see chapter "▶ Neanderthals and Their Contemporaries," Vol. 3) following a small amount of interbreeding (Green et al. 2010; Krause et al. 2010; Prüfer et al. 2013; Sankararaman et al. 2014) does not necessarily mean that they were not culturally modern, just as the extinction of local groups of modern *Homo sapiens* in recent times does not mean that they were not culturally modern. The main characteristic of *Homo* is that our cultural development can, and does, vary independently of our biological substrate (Conard 1990). Thus, late anatomically archaic peoples may or may not have been behaviorally modern, just as early anatomically modern humans may well have been behaviorally archaic (Zilhão 2001). Nonetheless, at the end of the day, only modern humans survived and populated all regions of the globe and outcompeted all other hominins.

In the coming years, archaeologists and paleoanthropologists need to establish high-quality regional databases and specific local scenarios and hypotheses for the evolution of modern patterns of behavior (Hublin et al. 1996; Parkington 2001; Lewis-Williams 2002; Conard and Bolus 2003; Longo et al. 2011; Higham et al. 2011, 2012; Douka et al. 2012; Talamo et al. 2012). As work progresses, researchers should be able to test these hypotheses and better define these diverse regional scenarios to create new models that come closer to reflecting the evolutionary reality that a nuanced history of our species warrants. This work should precede using multiple analytical paradigms and shifting scales of analysis (Conard 2001a). There are certainly multiple approaches to this complex problem, and all contextually informed explanatory models for the rise of cultural modernity are welcome, regardless of whether they originate from the natural sciences, social science, or humanities.

Regardless of where one positions oneself in these debates, only Paleolithic archaeologists and paleoanthropologists are able to make direct observations from the past, and thus they are in the best position to explain how our species evolved. If we accept the fundamental unity of all living people, the question of when hominins became like ourselves remains a relevant question that cannot be left to experts in other fields, who have no direct observations and data from the past. Following this line of argument, we should use our privileged position as the producers and curators of knowledge about the past to continue to refine our models of how populations of modern humans with our remarkable cultural capacities evolved.

Cross-References

- ▶ Defining *Homo erectus*
- ▶ Dispersals of Early Humans: Adaptations, Frontiers, and New Territories
- ▶ Evolution of Religion
- ▶ Hominin Paleodiets: The Contribution of Stable Isotopes
- ▶ *Homo ergaster* and Its Contemporaries
- ▶ *Homo floresiensis*
- ▶ Later Middle Pleistocene *Homo*
- ▶ Modeling the Past: Archaeology
- ▶ Modeling the Past: The Paleoethnological Approach
- ▶ Neanderthals and Their Contemporaries
- ▶ Origin of Modern Humans
- ▶ Overview of Paleolithic Archaeology
- ▶ Phylogenetic Relationships of Hominids: Biomolecular Approach
- ▶ Quaternary Deposits and Paleosites
- ▶ The Evolution of Speech and Language
- ▶ The Evolution of the Hominid Brain

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Evolution of Religion

Matthias Herrgen

Contents

Abstract

The evolutionary perspective on religion aims to provide a naturalistic foundation for religious behavior, as observed both in recent cultures and in the cultural

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M. Herrgen (✉)
Philosophisches Seminar, Westfälische Wilhelms–Universität Münster, Münster, Germany

Philosophisches Seminar, Bergische Universität Wuppertal, Wuppertal, Germany
e-mail: herrgenm@uni-muenster.de; matthias@herrgen.net

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remains of our ancestors. Theoretical approaches vary from “positive” positions that describe religion as an adaptation to certain human needs and conditions during the evolution of social behavior to “negative” positions that develop nonadaptive stance, side-product theories, or simply talking religion down. In a longer perspective, adaptive features can be described as emergent features of cultural evolution (mysticism, ethics, myth, and ritual as domains of religion). The focus on religious cognition as mental architecture provides tools for the solution of enduring problems in the understanding of (ancestral?) hominids. As paradigmatic presuppositions may change (revalidation of group selection), and novel hypothesis is generated (superorganism, cognitive niche construction), recent theoretical work on the evolution of religion is enlarging our perspective on a tremendously complex topic that has mainly excited discussion of its cognitive aspects (cognitive science of religion). The vast bio-cultural complexity of gene-culture coevolution must be in the focus of any theory of the evolution of religion.

Introduction

When Darwin founded evolutionary biology by publishing *On the Origin of Species* in 1859, biology and even human behavior were already topics for the natural sciences. Dealing with religion, some authors tried to reformulate naturalistic approaches polemically against the clergy (Rádl 1909). Darwin, known for his agnostic attitude (although he studied theology in Cambridge), was fully aware of the tremendous consequences of his theory; widely known is his famous note to his friend Joseph Dalton Hooker that admitting it was like “confessing a murder” in 1844 (see http://www.darwinproject.ac.uk/): To claim that species are not immutable was the first step against a prevailing theological doctrine – the idea of man, so far depending on creation, was free to fall too. From the starting point “crown of creation,” as being on top of all creatures with an ontological foundation in metaphysical dimensions, man fell down to “a gipsy at the edge of the universe” (Jacques Lucien Monod, 1910–1976).

The new option and challenge was to describe mankind in a perspective of development (process) instead of creation (status). As Darwin assumed that “light will be thrown on the origin of man and his history” (Darwin 1859) by applying his theory of natural selection on man, even human behavior came out of the shade. In his 1871 work *The Descent of Man*, the first approach to a naturalistic view on religion, dealing with the question of the origin of faith, can be found. It contains two aspects: (i) it describes religious behavior as a human universal that depends on a natural and cultural development and (ii) the question whether religion – a *belief* in god – can be explained by natural evolution has nothing to do with the “higher question” whether god exists or not. The barking of “Braubach’s dog,” Darwin’s famous example in this case, is the key to understanding or misunderstanding the concern: The sunshade, moved by the wind, is the target of the dogs barking. Darwin estimates him thinking of some unseen agents moving the cloth.

The misunderstanding is the comparison of the dog's attitude to the unseen agent to the human approach to god. The quest is to formulate a theory offering the possibility to deduce the origin of the specific human behavior from a common ancestral behavior, shown in the dog's behavior as well. The third component, the hypothesis about the phylogenetic roots of the behavior formulated within the methodic approach, is open to modification, discussion, and falsification. Darwin's fear about "committing a murder" was already mentioned in his letter to Hooker, showing his awareness about late effects of his theory – a methodological self-reflection. Furthermore, he was sensitive to the fragility of religious belief system. He acknowledged the religious practice of believers, as treating their world outlook with respect he refrained from attacking religion. In a letter to Karl Marx (1818–1883), he confessed in October 1880: "Incidentally, it is possible that the thought has influenced me here over charge to the pain I would cause some members of my family when I would start to support direct attacks on religion one way or another."

As a milestone towards the theoretical and empirical work of the cognitive and evolutionary psychology of religion, William James focused on *The Varieties of Religious Experience* (1902). While nineteenth-century philosophy was dealing with religion in terms of an anthropological need (projection of an idealized being as god, Feuerbach) or social construction (Marx, Durkheim), the focus was on the psychological phenomenon of religiousness. As an individual experience, they are as well part of our biological bias, depending on our social organization. In this view, even the evolution of religious behavior must have a story of a successful evolutionary development, keeping Dobzhansky's formula "nothing in biology makes sense except in the light of evolution" in mind (Dobzhansky 1973). Whether this process is adaptive or was adaptive may for now be an irrelevant one (some biologists tried to develop pantheistic theories of the evolution of religious behavior in man, introducing *Homo sapiens* as the praying animal, putting him on the top of a teleological evolution with a gnosis-enabled species on top (Hardy 1979)), more important was the foundation of a new background theory for discussing religion: the shift from religion (in a theological and institutional/sociological sense) to religious behavior. The belief and practice in orientation to supernatural beings and powers were open to scientific exploration, independently from the ongoing discussion about their existence. The proof of god's existence became irrelevant – no wonder the integration of an evolutionary history of religious experience into epistemological and theological approaches of religion is sometimes misunderstood as a challenging provocation. Nevertheless, the history of natural sciences, especially human biology, reminds of the need for responsibility. Naturalistic approaches have to be clear in their declaration of intention. When Baudy is offering a paleoanthropological theory of religion, talking about a "paleophysical space consciousness" and the developed feature of a "scenic amendment" as adaptation to Pleistocene environments (Baudy 1997) that are still vitalized today, he is offering a theory of *psychological components* as candidates for the theory of the evolution of religion. When Trinkaus is interpreting *archaeological reports* of burials, grave goods, or even early temple sites (Trinkaus 1985), he is reconstructing the visible but highly fragmented path from our ancestors towards nowadays religious routines. Nevertheless, both aspects are under the retention of being a "just so story," meaning paleo-poetry with a highly narrative component. On the one hand, theoretical assumptions tend to develop "easy to tell"-Panglossian arguments, and on the other hand, interpretations are addicted to their theoretical background and the zeitgeist – both are far from being constant. Compared to other topics in naturalistic explanations (evolutionary ethics, evolutionary epistemology, and evolutionary aesthetics), religion as issue holds a human self-understanding that goes far beyond "topics." Is a description of a "religious nature" – irrespective of being an adaption or not, increasing fitness or not – a substitution of a non-scientific self-understanding by just another story?

Aspects of Religion

Behavior and Evolutionary Psychology

Evolutionary psychology seeks for human psychological traits that are evolved adaptations – therefore, it can be seen as a long-term consequence of Darwin's approach to human nature as part of a natural history by means of natural selection. Human psychology is described as a functional product of natural or sexual selection, like in other approaches of adaptation (in mechanistic perspective on body parts like heart, brain, and blood circuit), the body is modularized, some evolutionary psychologists are arguing that the mind has a modular structure as well: modular adaptations are "invented" for different functions, offering the background for the Spandrel Theory: much of human behavior is the outcome of psychological adaptations that evolved to solve problems in human ancestral environments long time ago. The so-called adapted mind (Barkow et al. 1995: The Adapted Mind. Evolutionary Psychology and the Generation of Culture) pairs fragmented brain *functions* with estimated environmental needs and challenges of our ancestors (see Table 1 for an overview).

More astonishing is the observation that religious commitment often leads to a costly behavior: The participation in rituals takes time and is sometimes risky; a lot of religious systems define certain rules for their members and specialists like celibacy, leading to a poor reproductive success. Even practical costs for displaying a commitment come into count, reaching from sitting in silence to suicide bombing. One major task for evolutionary explanations is clear: The benefits of religious behavior must somehow outweigh the harms mentioned above. Even if the candidates seem to be clear (social bonding, explaining our origin, moral systems, etc.), the problem is still related to the cost problem, one component of the explanatory level. The evolution of religion in a perspective of evolutionary biology and psychology therefore deals with several sets of problems, connected to aspects of the religious behavior of human beings, populations, and institutions. They are confronted with a set of theories and theoretical frameworks aiming to provide a scientific background for the explanation of their development and functionality.

Table 1 Problems and explanatory components of religious behavior

Aspects of religious behavior	
Problems	Explanatory level
Cooperation	**TMT** (terror management theory) (Jonas and Fischer 2006)
Free rider	**MCI** (minimal counterintuitivity) (Purzycki and Sosis 2010)
Costly signaling	**PA** (punishment avoidance) and
Punishment	**CE** (cooperation enhancement)
Punishment avoidance	**SP** (supernatural punishment) (Schloss and Murray 2011)
Monitoring	**SM** (supernatural monitoring) (Bering 2011)
Credibility	**CREDs** (credibility enhancing displays) (Henrich 2009)
Agency detection	**ADD** (agency detection device) (Boyer 2002)
Cognition and metaphysics	Kinship imagery (Batson 1983)
Expenses, investment	Niche/niche construction (Bulbulia 2008)
	Memetics (Aunger 2002)
	Cultural group selection (Wilson 2002)
	Cognitive capacities of
	Folk mechanics
	Folk biology
	Folk psychology
	Attachment theory
	Intuitive ontology
	Genetics (**VMAT2**) (vesicular monoamine transporter 2)
	Spandrel
	Cost problem, investment
	Level of selection (individual, group, multilevel)
	Evolution of single components

Empirical and Practical Aspects

Testing theories about religion is nothing new: The effect of prayer to the sick was the concern of Francis Galton, Charles Darwin's first cousin. In 1872, he is – first of all – confronting presumptions about theology and religion with empirical (or rather statistical) facts, offering verifiable theories: "An unscientific reasoner will be guided by a confused recollection of crude experience. A scientific reasoner will scrutinize each separate experience before he admits it as evidence, and will compare all the cases he has selected on a methodical system" (Galton 1872, p. 125). His conclusion is that "It seems to me clear that all belief in the efficacy of prayer, in the sense in which I have been considering it, must be yielded also." Galton issues two caveats to the physical efficacy of prayer: (i) prayer can provide emotional catharsis through the act of self-expression and (ii) his study does not disparage the possibility of communing in one's heart with god. Assertion (ii) is presented with several constraints around the interference of imagination and personality, but Galton concedes that calm contemplation on the ideals of fellowship, responsibility, and the creative heritage of humanity have "much in common with the effort of communing with a God." In recent works, the alliance between religion and healing became a major topic; the ethnological report shows a large variety of techniques to seek for healing: Meditation, ecstasy, hypnosis, and trance stimulate neurophysiological processes with traceable effects on subjective well-being and health. As some techniques require the assistance or good will of higher-order powers, experts are released from other topics in order to focus on their magic business. It is an open question; if shamanism is the origin of medicine or religion, perhaps both are intrinsically tied together. All recent discussions about the placebo effect still show perplexing results about the magic of a cross-scored tablet; the belief in the substance is the key to the success of the therapy – no matter what the pharmacist tells us about the "true" impact of the substance. On a larger scale, some authors describe a positive correlation between the coping and handling of diseases and the creation of a "positive meaning" based on principles of faith. Coping with contingency is an easier task for the believer; the assumptions of their confession protect them from using a "psycho-hygienic function" (Voland 2010). Demographic studies show doubtless the reproductive success of denominations; they provide a shared rationalization and an intriguing motivation to engage in future projects and producing offspring (Blume 2009). On the other side of the coin, religions do not only disengage fear from the believer, but under certain circumstances (and dispositions), they might endow it. Not only in brute communities like Colonia Dignidad but even in psychotherapeutic facilities a rising amount of patients seek release from fear, disillusion, or suffering from long-term consequences of brain wash they had to experience in their communities. The development of a religious psychosis is as well possible without any despot forcing members of a group to perform certain actions declared as god's wish or ecclesiastical need. A rather new phenomenon is the "market of possibilities" of religious expertise and components, leading to a modal system of religion. Therefore, religious practice becomes an eclectical combination – of incompatible constituents? Many western European believers "on the edge" of established confessions seek inspiration and techniques of spiritual self-awareness in "eastern" meditation techniques. A lot of them simply do not come back, as therapists indicate a growing number of candidates lose their self-awareness in certain meditation techniques that plumb the "how far can you go" without a net. What might be an easy task for a Buddhist novice – losing the thought of a certain self in meditation – can destroy a callow self-consciousness orientated on other ideals and figures from an incommensurable cultural background. Psychiatrists discuss the work field between the keywords "god-intoxication" and "religious-medicine"; on the one hand is the Freudian perspective on religious beliefs as pathology outdated (Navratil 1992), while on the other hand is as well much work to do with questioning the options of integrating religious aspects in therapeutic treatment.

Evolutionary Anthropology and Primatology

The nature versus nurture debate may be the major underlying conflict between natural and social sciences. A change in the scientific approach through changing methodological axioms led towards a renewed understanding of anthropological sciences. It was in the 1950s when Sherwood Washburn (1911–2000) and Theodosius Dobzhansky (1900–1975) arranged the Cold Spring Harbor Symposium. It was a switch in the fixation of anthropologist from ideally race standards and characters (ancestors of idealistic morphology and race theory) to the observation of living populations, published in the epochal anthology *Anthropology Today* (Kroeber 1953). In his contribution "The Strategy of Physical Anthropology," Washburn outlines his theory of a new research approach by a theory-based *comparative biology*, including living relatives out of our pedigree: primates. The exploration of phylogenetic traits of human behavior became a major topic ever since the approaches of primatology, evolutionary ecology, and behavioral biology brought innovative impulses to anthropology. Especially recent works in the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany) contributed remarkable findings regarding the origin of social behavior, speech, social cognition, and, reaching deep in the humanities, the "theory of mind" (Tomasello 1999). The subject matter can be roughly named by referring to the term *human universals*, as from a different viewpoint, ethnologist Donald Brown calls the outcomes of his cultural-comparative screening of populations. Besides all cultural variations, our species can be described by a certain set of universals we all share (Brown 1991). Universals are nontrivial patterns of behavior that can be observed in all known populations; sexuality, for example, is trivial, as a reproductive need and a basic definition of life, but a code of conduct regulating sexual issues is a human universal. In a phylogenetic perspective, research programs trace the roots of these habits in comprehensive studies of our ancestors, living and extinct. This linking can be pursued to basic religious questions in primatology research. In recent works, primatologists observed the handling of deceased members of primate societies, especially newborn, establishing a vague sketch of primate thanatology in the genus *Pan* (Anderson et al. 2010).

In Wilson's Sociobiology, we find that "the enduring paradox of religion is that so much of its substance is demonstrably false, yet it remains a driving force in all societies. Men would rather believe than know, have the void as purpose, as Nietzsche said, than be void of purpose" (Wilson 1975, p. 561). The falsehood of the "substance" religion is an open question, as in the theoretical view of sociobiology, only the outcome counts: Religious behavior is open to empirical questions, estimating the impact on fitness of any observable behavior. In this approach, we can further on investigate whether religion can be seen as an adaptation (increasing fitness) or not (decreasing fitness).

Cognition and Metaphysics

Studies in the developmental and cognitive psychology offer some interesting aspect of childhood. Up to the fifth year, cognitive strategies can be described that offer religious convictions: All things have a function: birds fly, trees grow, and the sun heats. Kids estimate a knowledge of everything in every being simultaneously with their own perception: You cannot see me when I cover my eyes with my hands. This phenomenon of an imaginary shared perception will slightly fade away, partly substituted by the theory of mind (mind reading) in later child development (Tomasello 1999). This can be linked to a main issue of religious metaphysics: the existence of an all-knowing and ubiquitous observer. In this view, kids are intuitive theists, therefore carrying moral dimensions. (This changes the perspective about "learning" a religion, there is no need to adopt this ontological setting, and it is rather to scrutinize as a rationalist.)

Other problems of the cognitive competences are easy to handle by estimating their adaptive value: The "agent detection device" (ADD) leads us to imagine an agent behind natural events – the branch of this bush is moving; there must be a (unmoved) mover, a *prima causa*. It may be an advantage to take precautions than to ignore it (agnostic ignorance); like the threshold of a smoke detector, it has to be calibrated low enough. This may sound like early stages of animism; the relevant news in here is the fact that we talk about a synthesizing performance of an adapted brain, generating a world view based and calibrated to the environment. The discussion of the theomorphism of man or the anthropomorphism of god is the intellectual field of work, introduced by Feuerbach's projection thesis. They can be linked to the relevant aspects in cognitive sciences – like many other aspects represented in the so-called cognitive sciences of religion (CSR). Some authors expand ADD to a "hyperactive agent detection device," when the benefits of agent detection establish over phylogenetic time, leading to theories explaining why we see "faces in the cloud" (Guthrie 1995) and pass the Rorschach test, opening the approach to empirical testing as well.

Approaches to Religion

Defining Religion

There is a dialectical tension between the scientific and humanistic contents of anthropology. The natural scientist is aiming to give it all a mandatory twist, searching for structures, systems, and principles of all living things. It is an ongoing debate in the theory of sciences, whether biology (recently called "a science of specific solutions") is still a natural science. The challenge of evolution lies in a high degree of complexity as the only changeless component is variation itself. Evolution is a fundamental process of life; the theory holds an expansive force of integration to other scientific disciplines outside the channels of natural sciences. In technical, social, and cultural sciences, the theory of evolution has a late effect. "Darwin's dangerous idea" became a "universal acid" (Dennett 1995).

This aspect – working on specific questions and tasks in detail – is rather ignored in the clean environment of a laboratory. As many reductionists develop mandatory thesis, for example, claiming spin-off products of brain functions, the focus leads to an isolation of doubtless functional parts from environmental needs and conditions. This may satisfy the wishful thinking of the *one* reason that must be – but thinking some steps further shows that it cannot hold position against the complexity of the problem on all scales: The humanist aspect of anthropology simply cannot live with an under-complex explanation of our "human nature," starting from our self-understanding as cultural beings to the need for a free will to fulfill ethical issues. The problem of defining religion takes place in this minefield: It is not a physical object we can lean over; it is not only the human "on its own" like in the problem of philosophical anthropology; when the *explanans* is coincidental to the *explanandum*, the subject of explanation is equal to the object of explanation. Religion is unquestionable observable in its behavioral outcome – but this is a tip of the iceberg, still holding a lot under holy water. The horizontal line in this picture is a metaphysical metaphor, a spell that has to be broken (Dennett 2007) to have a closer, a scientific look at the underwater part of religion. Therefore, theories estimate the ways religion is and works, not as a separate entity but as "culture- and time-bound discursive properties" (as Stausberg puts it in Stausberg 2009).

In his 1921 published study *The Psychological Study of Religion: Its Origin, Function, and Future*, James Leuba (1867–1946) offered 48 different definitions of religion – it may be helpful for scientific history to continue collecting and detecting shifts in methodological and epistemological approaches. A brief and more or less classic definition that fits our needs is from William James (*The Varieties of Religious Experience* 1902:31):

> Religion, therefore, as I now ask you arbitrarily to take it, shall mean for us *the feelings, acts, and experiences of individual men in their solitude, so far as they apprehend themselves to stand in relation to whatever they may consider the divine*. Since the relation may be either moral, physical, or ritual, it is evident that out of religion in the sense in which we take it, theologies, philosophies, and ecclesiastical organizations may secondarily grow.

Feelings, acts, and experiences are the candidates to analyze for religious commitment. As religion thereby is bound to a subjective and substantiate expression in cognitive, social, and emotional processes, it is in reach for behavioral studies. It would be heresy to assume that natural sciences aim to "biologize" religion, but it would be obscurantism to deny advancement in natural and social sciences searching for an evolutionary explanation of human behavior. To avert further damage, a theoretically framed and therefore falsifiable description has nothing to do with "explaining religion away." Unquestionable, a lot of authors expanded the framework of naturalism in the realms of reductionisms – a methodological fallacy.

Origin of Religion

The nature of things is often seen as being determined in an ontological and metaphysical sense. This must be understood without any historical index. As mentioned in the essentialist's perspective, this is not the approach of an evolutionary perspective of religion, offering a specific theoretical account. Religion is understood as an emerging quality; the theory aims to provide the components necessary to generate religious behavior under certain conditions. This is provided by the archaeological record, discussing and interpreting early proofs of religious behavior by reconstructing burials, frequent use of cult sites, or other outcomes of human activities that somehow leave traces (Lewis-Williams 2010; Burkert 1996). Therefore, the origin of religion must be seen in its difference to the beginning in terms of evolutionary appearance. This dualism is a variation ever since the option of questioning religion was enriched by opening it to psychological aspects. When William James described the "The Varieties of Religious Experience" (James 1902), he clearly distinguished two questions: "What is the nature of religion?" and "What is the meaning of religion?" The nature of religion became a psychological problem, dealing with a large variety of the possible forms and attributes of higher forces, seen as an intrinsic factor of human psychology. No need to look for the nature of gods and supernatural actors if there is evidence for its origin in the human mind. But interpreting a cromlech as a religious site or cave art as a meaningful painting in terms of a religious fact demands a theoretical presumption, enabling us to name it. Therefore, we take it easy to classify things as religious in a historical perspective, leaving the question of its origin open. In other words, we define the facts widely sporty, but spare their formation condition.

Components of Religion

The idea of components of religion is fully dissolving the long-lasting perspective on religion as a unit sui generis. The religionist argument aims to keep theology prior to anthropology; the dissolution of religion into anthropology is the worst case scenario. Wrecking religion into functional components is wrong in Eliade's view, because "a religious phenomenon will only be recognized as such if it is grasped at its own level, that is to say, if it is studied as something religious. To try to grasp the essence of such a phenomenon by means of physiology, psychology, sociology, economics, linguistics, art or any other is false" (Eliade 1963, p. xiii); the "big picture" would be missing.

On the other end of the scale, the components as such may be accepted as separate units appearing in the human mind, but the existence of the one thing called religion is seen as an illusion. Religion needs construction! Boyer argues for the continuation of the Aufklärung, when Kant showed that religious ideas are creations of the mind. Religious studies need to go further on; with "the use of better science" they have to "show that the very existence of something called 'religion' is largely an illusion [. . .,] the package does not really exist as such. Notions of supernatural agents, of morality, of ethnic identity, of ritual requirements and other experiences, all appears in human mind independently" (Boyer 2010, p. 1). In this case, religion is not subject to methodological fragmentation prior to theoretical needs – it is denied ontologically; it is an "airy nothing." Such programmatic perspectives on continuing the Aufklärung are worthy of discussion; moreover, they lay open the omnipresent caveat that science sometimes carries the intention of dissolving religion. Still they provide new spheres of action: The cognitive sciences of religion offer a set of a cross-culturally recurrent universal cognitive mechanisms, a “cognitive gear” of religiousness (afterlife, beings with special powers, signs and portents, creationism, spirit possession, rituals, ritual exegesis, the sacred, deference, moral obligation, punishment and reward, and revelation) (see Whitehouse 2008).

Domains of Religion

The modular structure of cognitive skills can be described as a network of brain, body, language, and culture (Mithen 2007). They discuss the human instincts as a biological universal feature of human behavior and wit. Their developmental history offers the explanation theory of evolutionary psychology: The environment of evolutionary adaptedness (EEA) leads to Darwinian algorithms, allowing predictions about processes of adaptation, hence to reconstruct past adaptations by formulation hypothesis (an architecture underlying the human capacity for religion). The evolutionary approach to religion supposes that human phylogeny provided a cognitive integration of the four domains: mysticism, ethics, myths, and ritual (see Table 2 for an overview). In this combination, religiosity emerges as an evolutionary adaptation providing reproductive advantages (see Voland and Söling 2004). Religiosity proves to solve the problems underlying the domains in individual and collective perspective: Individually experienced contingency is answered by commonly shared mysticism. Social interaction is regulated and to a certain degree predictable, enabling human societies to invest in long-term and large-scale projects. The myth provides patterns and externalized powers or agents as templates for commitments, enabling the identification of group members and the detection of free riders. The ritual is the hurdle that has to be taken to fulfill expectations regarding a trustworthy confession to a group, paid back in the offered earthly or heavenly benefit. It may be expected that the selection pressure on religiosity potentially played a major role in human evolution when the population count exceeded family sizes and the competition between groups were judged by its efficiency, competences, and – “naturally” – fitness.

Table 2 Domains of religiosity (see Voland and Söling 2004)

Domain	Mysticism	Ethics	Myth	Ritual
Adapted for	Intuitive ontologies	Social systems	Language instinct	Handicap
Function	Categorization	Social competence	Group communication	Trustworthy articulation
New function	*Coping with contingence*	–	–	–
Differentiation	Assuaged decision-making	Allowing cooperation benefits	Social identity, in-group/out-group differentiation	Combating fraud, detection of free riders

Mysticism

The underlying Darwinian algorithm of mysticism is the competition of intuitive ontologies. They evolved as a coping strategy with unknown components of the surrounding environment – the human mind dependently needs “facts” for judging situations and making decisions. We need to know why the branch of that scrub is moving – the ontology that offers the wind as the one and only explanation will not take the predator into account, proving as a bad explanation. As Tomasello showed in comparative studies, it is most likely that intuitive ontologies are based on social experiences and developed for the need of judging and categorizing social interaction partners. Social detection categories, hence social ontologies based on human agents, are transferred into the natural environment. Our *theory of mind* (ToM) is on the one hand a feature of human evolution; in comparative studies with primate infants, specific human features of detecting intentions are shown (Bullinger et al. 2011). Infants do not only recognize intentions of social partners clearly, showing that the anticipation is based on mind reading as part of our evolved features of our mind. They even tend to assist and therefore invest in the action of the social partner, as long as the execution of the action is hampered by anything only the infant can bring in order. Ontogenetically, the ToM will be calibrated to cultural patterns and social conditions – but we are born as dualists, animists, and “intuitive theists” (see Knight et al. 2004) and think teleologically. On the other hand, the ToM proved as a high-capacity mechanism of the human brain that in general can prove as helpful even in nonsocial conditions; treating nonhuman components as actors can offer ontological concepts that may be incorrect from a distant perspective. But the Darwinian algorithm is not selected for truth, it is selected for effectiveness; as long as the intuitive ontology generates a helpful representation of the environment, their outcome will determine our world view.

Ethics

The question concerning the evolution of altruistic behavior and the establishment of morals is probably the eldest topic in evolutionary biology. As Mayr points out in his philosophy of biology (Mayr 1998), it was already clear to Darwin that altruistic behavior cannot be explained by survival of the fittest alone. Studies about the pattern of cooperation in groups, mathematical models, and investment theories concerning grades of blood relationship (Alexander 1987; Hamilton 1964) showed that patterns based on kinship soon become inappropriate. Stepping over a threshold in respect of group sizes blasting family boundaries, new challenges and behavior patterns arise: *Homo confidens* meets *Homo mendax*. As gene altruism will not handle this encounter, socially established rules regulate interaction. The observance of ethical rules and the punishment of deviant behavior are facilitated by assuming a higher power observing even unseen behavior. A hypothesis claims the belief in god as a program of internalizing moral rules. The external judge becomes irrelevant as long as the sanction of deviant behavior, or even thoughts, is happening in the head. Voland assumes that religion donates morals, not understood in a theological sense that refers to metaphysical values shown in revelation. It is rather a social technique, because fear from punishment makes "good behavior" more probable.

Myth

The function of myth as a social-bonding technique is a double-edged sword: The enhancement of group solidarity and identity must pay a price (the dissociation of out-groups). Members of any unknown collective are screened; as long as they do not match with the standards provided by the own myth or mythical tradition, xenophobia will be a relevant variable. Judging whether someone believes in the same god, therefore is a trustworthy social partner, becomes a feature-depending friend- or foe-decision-making system. The decision is not based on features relevant to cooperation or factual investments, like treated in tit-for-tat systems or other models in game theory (Luce and Raiffa 1989). In a new cultural niche – a niche that is not occupied, but constructed (see section "(Cognitive) Niche Construction") – specific displays and commitments are the key to social acceptance in an idealized group of believers.

Many social scientists showed in early critiques that religion can be described as a highly functional social phenomenon – regardless of any theological aspects (see Durkheim 1981 [1912] for a functional approach and Luhmann (2002) for the orientation function of religion in system theory). Basic social patterns of behavior, social order, and "naturally" language depend on speech; thence, the part of the relevant sacral components in the appearance of these features must be evaluated.

Ritual

Rituals improve the cohesiveness in groups. When special occasions in biographic situations (birth, marriage, *rites de passage*, funeral), social events with political functions (coronations, elections, executions), or festivities in the circle of the year happen, certain patterns of behavior are expected. The repeatability of these events, observable in all known cultures, leads to precise expectations for all participants. The more complex the rituals become, the more the staging will lead to a stratification of its members. In case of magic rituals, aiming to quest or pray for support from higher powers, special castes may arise (shamans, priests, etc.). Besides the memorable and frequently repeated pattern with a clear purpose, rituals are creating sense. They are not only a component in utilitarian structures, they generate and play a key role in social communication, providing conventions. The participation in rituals is associated with the handicap principle. Rituals require investment; only who can afford and is willing to pay the price proves to be a member (see Zahavi 1975; Zahavi and Zahavi 1997). Rituals offer solutions for common problems of social interaction like free riders and cheaters (see Table 3 Cooperation Problems and Solutions).

Table 3 Cooperation problems and solutions

Cooperation problem	Solution	Ritual
Free rider, cheater	Profane punishment	Court
Missing criminal prosecution	Supernatural punishment	Worship
Disbelief	Costly signals	Offering, initiation
Hypocrisy	Showing emotion	Ecstasy, fear
Self-deception	Internalization	Soul-searching, confession

Recent Theories of Religion

In a first overview, we can structure the landscape of evolutionary explanations of religion in two groups with explorative subdivisions and exemplary authors/contributions.

Nonadaptive Theories

Nonadaptive theories describe religion as a useless or even dysfunctional product or by-product of specific mental processes. These processes might be adaptive in other circumstance, but they are not used as intended. Praying for rain will not let it rain, but praying in a group for rain will intensify the social cohesion. Nonadaptive theories may see religion as a neutral feature, developing independently from cultural evolution. The worst case scenario argues for a cultural parasitism: Cultural features spread as cultural parasites (*memes*) *without any selective advantages for individuals or groups.* (*See Table 4 for an overview and scientific representatives.*)

Alexander suggested that religion is a legacy of our phylogenetic heritage (Alexander 1987). As our behavioral fixture has been developed in specific needs and circumstance, it is related to Paleolithic group sizes and social structures, incommensurable with nowadays social systems and therefore adapted to the wrong thing. This is supplemented with arguments from population genetics, as the genetic variation in huge social systems leads to genetic distances within groups, undermining altruistic investment in the same lineage – the currency of fitness.

Religion as epiphenomenon describes religious behavior as based on functional criteria different to religious purposes. Like the spandrel in architecture, the “beautiful” ornament has nothing to do with structural analysis. The conception of the spandrel became a hot selling item, depending on the corner it is decorating. This argument is also known as the Panglossian argument, recommitting on the so-called figure in Voltaire’s Candide (1759), and was first brought into discussion by Steven

Table 4 Systematic overview: evolutionary approaches to religion

A Religion as nonadaptation	B Religion as adaptation
A1 Outdated adaptation	**B1 Individual selection**
Ancient sexual selection	Evolution of single components
Euler (2004): Sexuelle Selektion und Religion	Söling (2002): Der Gottesinstinkt
Phylogenetic heritage	Evolution of cognitive abilities
Alexander (1987): The Biology of Moral Systems	Saroglou (2010): Religiousness as a Cultural Adaptation of Basic Traits [**FFM**, five-factor model (Extraversion, Agreeableness, Conscientiousness, Neuroticism, Openness to Experience)]
	Intuitive ontologies
	Purzycki and Sosis (2010): Religious Concepts as Necessary Components of the Adaptive Religious System
	Genetic disposition
	Hamer (2004): The God Gene
A2 By-product	**B2 Group selection**
Cultural parasitism by memes (religions as memeplexes)	Kinship imagery
Blackmore (1999): The Meme Machine Aunger (2002): The Electric Meme	Batson (1983): Sociobiology and the Role of Religion in Promoting Prosocial Behavior
Cognitive parasite	Cooperation enhancement
Atran (2002): In Gods We Trust	Schloss (2008): He Who Laughs Best: Involuntary Religious Affect as a Solution to Recursive Cooperation Defection
	Group (and multilevel) selection
	Wilson (2002): Darwin's Cathedral
A3 Spandrel	**B3 Niche construction ability**
On mental capacities	Niche construction
Boyer (2002): Religion Explained	Bulbulia (2008): Meme Infection or Religious Niche Construction? An Adaptationist Alternative to the Cultural Maladaptationist Hypothesis
Boyer (2010): The Fracture of an Illusion: Science and the Dissolution of Religion	
"Faces in the cloud"	
Guthrie (1995): Faces in the Cloud. A New Theory of Religion	
Neurotheology	
Persinger (1987): Neuropsychological Bases of God Beliefs	
Third Cartesian world	
Newberg et al. (2005): Why God Won't Go Away: Brain Science and the Biology of Belief	

J. Gould and Richard C. Lewontin (Gould and Lewontin 1979: The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme).

In Scott Atran's *In Gods We Trust*, many distinctive research programs in social, cognitive, and historical sciences, all linked to their evolutionary character, are woven together and tested on empirical studies as well. In combining cognitive sciences and evolutionary psychology, his focus is on the cost aspect of religious behavior; many seemingly do not pay out. Hardly surprising, his starting point is a denial of religion as a dedicated "religious faculty" in human cognition; therefore, no religiosity can be supposed as disposition: "Religions are not adaptations and they have no evolutionary functions as such" (Atran 2002, p. 12). Our hands did not evolve for holding a computer mouse; they are adaptive to these purposes but are not adaptations for them. Same with religion, "Religion may be adaptive in some contexts without being an adaptation in an evolutionary sense"; his thought experiment introducing religion as a river flowing through a varied landscape is a good attorney in fact for nonadaptive theories: "the class of humanly plausible religions is one set of paths in the landscape's drainage basin" (Atran 2002, p. 11). The topography of the land is made out of calibrated human brain/mind functions as speech, vision, theory of mind, folk biology, folk psychology, and many others representing peaks. The river, a flow of conceptual information, rushes through the human intelligence; the topography (the peaks as mentioned above plus other factors like weather, the place holder for any inputs in this big picture) causes the river to flow certain ways. If it flows long enough, we might even expect a river bed. A main quest concerns development and consolidation of religious concepts. On the one hand, the development of these concepts (like gods, agents, and spirits) has to be explained, and on the other hand, it must be linked to the costs as far as these beliefs lead to certain behavior. From an evolutionary perspective, the genesis of these beliefs is not sufficient; selection's tolerance for the real costs must be brought to the table as well. The minimally counterintuitive concept (MCI) is offering a theory about our abilities to understand and memorize religious concepts. Ordinary concepts receive a slight modification, thereby compel attention; in a perfectly condensed phrase by Bulbulia, "Religion is the *familiar*, made *strange*" (Bulbulia 2009, p. 160), leading to absurd commitments. As soon as these concepts are alive and become a salient feature in a specific group, the evolutionary fate depends on the survivability of the concept. Results of early empirical studies suggest that recall effects may account for the recurrent features found in religious concepts from different cultures (Boyer and Ramble 2001). This links the evolutionary conditions of emerging to the explanation of religious behavior as well as the features of religious beliefs as a human universal. Known ontological categories, imbedded in folk mechanics, folk biology, and folk psychology, have to be violated in order to be counterintuitive. Depending on the class of objects (persons, animals, plants, artifacts, and natural objects), (i) the estimated psychological qualities, (ii) the biological features, or (iii) the physical properties have to be violated. A growing plant will not make a deal, but an all-knowing, flying, and invisible tree will be a better candidate to be memorized.

Adaptive Theories

On the level of individual selection, religious behavior evolved for the benefit of the individual in comparison to competitors. On the level of kin selection, religious behavior gives advantage to genetically related individuals in comparison to genetically more distant group members. On the level of group selection, religion is selected for the evolutionary success of groups, favoring tools to improve willingness and toughness. (*See Table* 4 *for an overview and scientific representatives.*)

In social sciences, Durkheim and his trendsetting functional definition in his work *Les formes élémentaires de la vie religieuse* (Durkheim 1981/1912) became the framework for theories of religion as an adaptation. For Durkheim, a religious group is "a society whose members are united by the fact that they think in the same way in regard to the sacred world and its relations with the profane world, and by the fact that they translate these common ideas into common practices." The "translation" starts with cognitive processes and ends with practices; the collective consciousness is the consciousness of all individuals. This allows common practices and combined powers and affords for higher goals. Following this pattern will easily lead to advantages of groups compared to other less organized groups or even individuals compared to ones with lower involvement in religious practices. Nowadays, we can state that the critique of religion based on a historical coupling of religion and power misses the core of an obviously evolutionary disposition of religiousness.

Campbell sees religion as the solution for the "Darwinian paradox": The only way to restrain human selfishness lies within religion, promoting prosocial behavior and defeating egoism (Campbell 1975: On the conflicts between biological and social evolution and between psychology and moral tradition). In this perspective, the welfare of the individual is prior to the welfare of the group. Examples of elite privileges like priests running on the back of the laity show that this is not an endless game. Leaving the rudiment of individual egoism and changing the scale to a comparative analysis of groups – their bonding components, social cohesion techniques, and competition with other groups and their struggle for existence – we come to a major aspect of the functional aspect of religious behavior in an evolutionary outlook. The bottleneck of social evolution, long before sedentism, came along the natural selection among small units of groups in rivalry for ecological benefits. The existential competition between the groups promoted those with the best defensiveness and probably biggest group size. Evolutionary mechanisms to assure these features by restraining human selfishness and establishing investment in collective attitudes and strategies became the ones that paid out. Especially rituals can be observed in their functional role for group bonding; furthermore, this is not only in the field of expertise of anthropologists and ethnologists, as rituals in military actions, sports, and pop culture show the defining on motivational power of these elements. In this moment, groups are alive in their commitment and are defined by the emotionality of the social experience of being a part in something way bigger – as long as you are "in."

The self-understanding of a group therefore needs criteria for who is “in” and who is “out”; different authors place the myth on this place; sharing stories from a common ground explaining your existence and offering the metaphysical background of it makes you a member (see Voland’s four domains of religiosity, myths, mysticism, ethics, and rituals, in Voland and Söling (2004)). The myth is providing the truth as a strategic construction; in Voland’s approach, the aphorism of Karl Jaspers (German philosopher, 1883–1969) “truth is, what we have in common” has to be inverted: “what we have in common, is the truth,” a hypothesis why religions have to be dogmatic in order to conserve their group-defining myths. Others leave the solution of this topic to a more profane aspect, in commitment theories and behavioral strategies, providing cooperation enhancement by the development of credibility displays (Schloss and Murray 2011). Belief in supernatural agents is adaptive because these agents are all-knowing punishers. Belief in supernatural punishment can enhance within group cooperation, called “cooperation enhancement” (CE). Moreover, it can reduce cheating or free riding, called “punishment avoidance” (PA). In this approach, we can show that standard problems of interaction in groups request special methods of resolution, implemented in certain rituals (see Schloss 2008).

Superorganisms and Realism

A controversial contribution to evolutionary theories of religion may be David Sloan Wilson’s Darwin’s Cathedral, bringing back in models of group selection and explaining religion in terms of a “superorganism.” In his valuation, the term “organism” in the group context is synonymous with “adaptive at the group level.” After years of favoring the individual selection as leading paradigm in sociobiology, the “selfish gene” is getting some competition. Starting with George Williams’ “Adaptation and Natural Selection” (Williams 1996/1966) and the epoch-making “Selfish Gene” from Richard Dawkins in 1976 (Dawkins 2006b), phenotypes were seen as vehicles of benefit for DNA; selection’s targets were condensed to the genetic substrate. When “rethinking the foundations of sociobiology” in 2007, David S. Wilson and Edward O. Wilson put the finger on the 1960s, claiming pivotal events leading to a more or less intransigent rejection of group selection. In their view, multilevel selection theory (including group selection) provides an elegant theoretical foundation for sociobiology (Wilson and Wilson 2007). This is a major impulse for David S. Wilson’s attempt to develop an organismic concept of religious groups, bringing life in the new “gold standard” of sociobiology: “Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary” (Wilson and Wilson 2007, p. 345). His afford as well bears in mind that the functionalist perspective of evolutionary approaches leads to a methodological reductionism, even if evolutionary theories provide testable hypothesis about religion they might not hit the nail on the head. Hence, paraphrasing Kant, religious studies are blind without biological theory, and biological speculation is empty without scholarly data.

The standard perspectives of cognitive models are based on individualism, whether religion is generated by individual brains emerging religion in a group of individuals or even if the brain is infected by a Congo virus, a technique of memes to occupy human brains. In Darwin's cathedral, the first step, recalling the renaissance of group selection theories, is to claim an averaging fallacy, ruling out group selection by definition. But if a considered trait is a social behavior, "the fitness of an individual is determined by its own trait and the traits of the individual with whom it interacts. These individuals constitute the group, which must be identified accurately to calculate the fitness that determine[s] the outcome of evolution" (Wilson 2002, p. 15), showing clearly the concept of the enemy: a theory of evolution restricted to genetic evolution that sticks to the individual and restricted perspective on a pure gene carrier. His approach aims to reactivate the standard patterns of Darwinian evolutionary development and apply them for group-level adaptations by means of differential survival and reproduction of groups. From the perspective of the selfish gene, there was only one possibility for altruism to evolve: when average returns exceed average costs (see Hamilton 1964). The natural selection of groups will not play a role in comparing groups of altruistic and non-altruistic members, but in comparing *altruistic* groups, we can handle special patterns of human behavior and test hypothesis on religion as a group-level adaptation to enhance in-group cooperation (see Wilson 2005). The approach proposes that religious traits evolve to functionally integrate the behavior of all persons within a (we might then call it religious) group who share them. This is the underlying process that makes a "superorganism" out of it, offering another theoretical framework (like organismic biology describing units as systems) to solve problems of cooperation and coordination. Group selection therefore predicts culturally evolved patterns of behavior to prohibit selfish individualism within groups. It is a shift from a perspective of altruism-based social life to a certain mode of social behavior induced by social control: Monitoring, censure, punishment, and exile are the bricks that automatically request corresponding patterns of behavior like signaling (e.g., the theory of credibility enhancement displays in Henrich (2009)), playing a key role in understanding the evolutionary development and function of rituals. Wilson sees religious groups as rapidly evolving entities adapted to their current environments; therefore, religion is a solidarity technology, and therefore, religious variation will be limited by the purposes as targets of selection: the demand of building and ensuring a community. The question is still open whether the restricted diversity of religions (scholar evidence shows that religions are not set in stone, rather entities on a timescale in constant change) is better explained by the specific needs of optimizing human interaction or by mental habits of the *adapted mind*. "If the individual is no longer a privileged unit of selection, it is no longer a privileged unit of cognition. We are free to imagine individuals in a social group connected in a circuitry that gives the group the status of the brain and the individual the status of the neuron" (Wilson 2002, p. 33).

Evolutionary theories of religion offer a heuristic tool: The theory builds on the distinction between ultimate and proximate causes. Religion plays a key role in coping with reality; dealing with the world leads to a certain knowledge that can be called facts – and a certain set of features that derive or build the domains of mysticism and myth. Following this dichotomy set, two kinds of realism are introduced, a *factual realism* that accurately describes the world (irrespective of its functionality) and a *practical realism* showing useful beliefs, regardless of their validity to the "hard facts" they claim. In the perspective of selection, the factual realism is selected for accuracy, while the practical realism is selected as a biological utility for the effect of the belief. It has to be greater than the cost of holding the belief. This theoretical approach leads to a new framework for working with religious issues without explaining religion away. Even if evolutionary sciences have to be selective and therefore offer a reductionistic perspective, proximate behavior can be explained in a way that leads to the idea of being religious as a natural phenomenon. Compared to other critiques of religion that rather look like weapons against religions, this is a new standard in handling religion. Dawkins, for instance, describes the phenomenon as pathology: Infected brains, run by bad memes invoking religious behavior, take over the human being; therefore, religious behavior as well as the outcome of this "illness" (churches as institutions, castes, priests, mythology, and spirituality) must be treated (Dawkins 2006a). Dennett introduces religions as a carrier of "bad spells" and "toxic mutations." Only healthy people (better to be an atheist than an agnostic) do not show the symptoms (Dennett 2007). In the approach based on practical realism as instrument of social group organization, all of a sudden, the concept of an enemy loses ground. The claim of god becomes irrelevant; whatever the container of practical realism carries is selected for its positive effect of the belief. There is no pathology to defame beliefs and automatically favoring the disbeliever, rather the opposite: As the practical realism provides useful beliefs leading to fitness maximizing behavior on the group level, the outside disbeliever is under suspicion. The theory must handle the phenomenon of deviant behavior within a group or offer bypass theories to reach the goal of the intended behavior. Religions do not evolve for their accuracy, but they evolve to secure harmony. In this sense, we have an evolutionary foundation of moral systems and ethics, as well a theory to cope with the Darwinian paradox (the aporia of social behavior in a world of the survival of the fittest):

> We might therefore expect moral systems to be designed to trigger powerful emotional impulses, linking joy with right, fear with wrong, anger with transgression. We might expect stories, music and rituals to be at last as important as logical arguments in orchestration the behaviour of groups. Supernatural agents and events that never happened can provide blueprints for action that far surpass factual accounts of the natural world in clarity and motivation powers. (Wilson 2002, p. 42)

This deals with religion as a part of human culture, as stories and music can be read as representatives of aesthetical articulation and symbolical representation. Cassirer identified mythological thinking and perception as the fundamental symbolical form. The mythical explanation of the world, to continue his valuation, leads to emotions (cf. Wilson) that generate the phenomenon that myths will not come in objects but in physiognomic features. Hence, we can link the phenomenon of practical beliefs as a key feature of religious behavior to the larger frame of symbolical representation that enables the cultural development of man – and not vice versa. "Myth is filled with the most violent emotions and the most frightful visions. But in myth man begins to learn a new and strange art: the art of expressing, and that means of organizing his most deeply rooted instincts, his hopes and fears" (Cassirer 1946, p. 45). Cassirer denies that fear leads to religion as a mere product. There is more than fear as an "outcome" like myth and religion. "But what is most essential in man's religious life is not the fact of *fear*, but the *metamorphosis* of fear. Fear is a universal biological instinct. It can never be completely overcome or suppressed, but it can change its form" (Cassirer 1946, p. 45).

(Cognitive) Niche Construction

The coevolution of nature and culture is a debate about leaving the boundaries of a discussion focused on the gene as the driving force. The approach of Richerson and Boyd, claiming a cultural evolution "not by genes alone" (Richerson and Boyd 2005), brought a fruitful impulse beside other authors on the topic (Sperber 1996) in preparation for an extension of the niche conception. The concept of the niche was introduced to address key adaptation, enabling an organism to occupy ecological niches by applying organismic licenses. The picture of the niche has been extended to cognitive niches, therefore offering a mental construction of cognitive niches as a theoretical entry to handle cultural development in an evolutionary approach.

> Cultures are defensive constructions against chaos, designed to reduce the impact of randomness experience. They are adaptive responses, just as feathers are for birds and fur for mammals. Cultures prescribe norms, evolve goals, and build beliefs that help us tackle the challenges of existence. In so doing they must rule out many alternative goals and beliefs, and thereby limit possibilities; but this channeling of attention to a limited set of goals and means is what allows effortless actions within self-erected boundaries. (Csikszentmihalyi 1990, p. 91)

Proposed is a conceptual model that maps the causal pathways relating biological evolution to cultural change. It builds on evolutionary theory by placing emphasis on the capacity of organisms to modify sources of natural selection in their environment. Niche construction means influences on more than the ecological surrounding, even social and cultural parameters are changed; therefore, a feedback in form of changing selective aspects of selection plays a role in the process of cultural evolution. The evolutionary dynamics are broadened, allowing to incorporate ontogenetic and cultural processes. Individuals or phenotypes have a more active role, as laying hand on relevant elevating screws, compared to the standard assumption of a passive phenotype determined by genetic dispositions and environmental impact (see Laland et al. 2000; Laland and Sterelny 2006; Kendal et al. 2011). In this new level, not only the question concerning the positive effect of belief is formulated, but the question concerning the positive effect *of* the belief *on* the belief has a theoretical ground. Advocates of this approach argue for taking (cognitive) niche construction seriously: "there is both accuracy and utility in treating niche construction as an evolutionary process in its own right, rather than as merely a product of evolution. Niche construction may be influenced by genetic, ontogenetic and cultural information and feeds back to influence selective processes at each of these levels" (Laland 2009, p. 35). For the formulation of hypotheses on adaptive processes in human evolution, the organism-environment match can be addressed as a reciprocal interaction between various levels of natural selection and aspects of (cultural) niche construction. The phenotype, formerly seen as a passive taker of evolutionary processes, shines in a new light: "Now phenotypes play two roles in evolution, they survive and reproduce but they also construct and modify environments, modifying selection pressures" (Laland 2009, p. 37). Note that on the one hand, all arguments referring to an adapted mind – unfortunately to the requirements of our stone age ancestors – experience contrary wind and on the other hand, the phenotype as an environment modifier will play a certain role in telling "just so stories": The unsatisfying situation of judging adaptations as outcomes of adaptive processes ex post facto only, leading to a Panglossian circular argument, may be altered as the niche construction allows to deal with the process in the beginning. "Human evolution may be unique in that our culture and niche construction have become self-reinforcing, with transgenerational culture modifying the environment in a manner that favours ever-more culture, and niche construction informed by cultural knowledge becoming ever-more powerful" (Laland 2009, p. 39). This perspective may explain religious behavior as unique, because the cognitive construction of its components is self-reinforcing, with transcultural domains of religiosity modifying the social environment in a manner that favors religion in the cultural evolution of *Homo sapiens*.

Perspectives: On eReligion and iReligion

"The predisposition to religious belief is the most complex and powerful force in the human mind and in all probability an ineradicable part of human nature" (Wilson 1979, p. 169). Undoubtedly, there is no question: Religiosity can be seen as a human universal (see Brown 1991). But religion as a subject matter to science runs into a variety of approaches, each of them considering certain aspects of religiosity depending on the methodological background. Ever since psychology joined the disciplines working on this issue, the dictum of William James showed that different heuristics aim for different aspects. In his Varieties of Religious Experience from 1902, he made a distinction between two questions: "What is the nature of religion?" and "What is the meaning of religion?" It can be claimed that the search for the nature caused a vivid field of psychological research, following the assumption that the brain is the location and therefore the place religion "happens."

A recent nomenclature (developed by Joseph Bulbulia) addresses eReligion (the external aspects of religion, the behavioral and cultural outcome) and iReligion (innate religion). Rethinking the relationship of these matters shows the twist that the evolutionary perspective brought into the scientific discussion about religion. The long-lasting deduction of iReligion from the "sacred" eReligion justified an almost metaphysical standing of man as a religious-cultural being. The "big picture" was already in place – this is inverted in cognitive theories, when the fragmented inputs of iReligion reconstitute a religious culture. eReligion is the big picture *at last*, not set in stone from the beginning. But even if the twist brought new approaches, ideas of religious dimensions, and therefore new theoretical perspectives, an underlying dualism seems to be alive: the individual versus social realm of religion(s). For future perspectives on evolutionary aspects of religion, there is much work to do in reframing this problem in the challenging entanglement of nature and culture. Focusing on the recent works, introduced as des CSR, the new aspect of the relation between cognition and culture can be described as dialectic, but not as an antagonism. Referring to the prospects of a cognitive niche construction, the brain is no longer a hardware that is genetically determined to generate a culture by running a heritage program; it becomes a cultural and social artifact. There may be – a tribute to some more or less reductionist naturalists – a lot of biological and even cognitive processes out of reach of our consciousness. They provide the theoretical framework to formulate hypothesis regarding the time and ecological aspects of their development in the biological evolution of *Homo sapiens*. These models of hominization are the starting basis for mental options leaving the area of natural sciences. When symbolical representations take the lead, the click of the ratchet becomes a relevant one – not to be understood as a single event but as the progression from *hominitas* to *humanitas*, when upon biological features, the cultural articulation occurs. This leads as well to religious conceptualizations that clearly operate as symbols, and symbolization is a promising starting point to connect cognition and culture.

A question is whether we have to deal with an encapsulation of religious cognition as a methodological narrowness. As Lawson and McCauley already showed in the 1990s, a proclaimed *cognitive turn* in “Rethinking Religion: Connecting Cognition and Culture” introduced the fundament for the so-called cognitive sciences of religion (CSR; see Barrett and Burdett (2011) for an overview). If this leads to the indication of a narrow-angle glaucoma, all depends on the self-conception and level of methodological self-reflection of the participating disciplines. There is no antidote against the atheistically apodictic – but the increasing discussions and projects on theories of evolution, especially considering evolutionary approaches, speak for themselves. A lot of work ahead, there is no metatheory in sight, capable of combining the contemporary approaches. Not only scientific work has to be done, both scientists and believers (not to be misunderstood as dichotomy) have to learn from recent findings. There are new terms in circulation that may be unsettling, talking about sacred things that may sound defaming. Followers of religion must learn to accept that the progress in sciences creates a new vocabulary and theoretical framework. It may sound crude when Boyer calls religion an “airy nothing” – this will be misunderstood when interpreted as an attack on religion but reveals its true meaning when interpreted with the theoretical background of the coevolution of nature and culture. “Airy nothing” is a phrase out of Shakespeare’s *A Midsummer Night’s Dream* (Act 5, Scene1), when Theseus, the Duke of Athens, claims: “And as imagination bodies forth/The forms of things unknown, the poet’s pen/Turns them to shapes and gives to airy nothing/A local habitation and a name.” The unknown obtains a name: In the beginning was the Word (John 1:1). Besides new terms, religious representatives must accept that religious belief and behavior has not fallen from the sky, but is a natural phenomenon with a natural history that offers benefits to users that can be described within biological purposes. The relation between scientific explanations and religious belief changes as well as the foundations for a false peace. Obstacles like the NOMA proposition (the theory of science and religion as Nonoverlapping Magisteria; see Gould 1997; 1999) proved to be incorrect – rather a spell from the inside that has to be broken, there is no need to take evolutionary biology on a leash. Atheists and some other Brights must acknowledge that religiousness as a natural phenomenon shows certain features and abilities in social systems and might be requested from believers, even in modified form from disbelievers, because its functionality is based on the intrinsic motivation of the human mind generating religious life, practice, and perspective. "It is no obligation to belief; but to act as if you belief." [„Es ist nicht Pflicht, zu glauben, [. . .] sondern es ist bloß und allein dies Pflicht, zu handeln, als ob man es glaubte"Friedrich Karl Forberg (1798, p. 38).

Conclusion

The evolutionary perspective on religion combines research findings and theoretical approaches to test the hypothesis that human religiousness may arise from a vast variety of adaptations in the evolutionary history of *Homo sapiens*, observable both in recent cultures and in the cultural products of our ancestors. Theoretical approaches offer 'positive' positions that describe religion as an adaption to certain human needs and conditions during the evolution of social behavior, providing solutions for cooperation problems in complex communities. They include improving the ability to cope with crises and to overcome the attraction of personal gain by exploiting others; avoidance of harming the common good; improving cooperation and moral solidarity within groups; and improving competitiveness with other groups. So-called domains of religiosity (mysticism, ethics, myth and ritual) describe a modular structure of cognitive skills in a network of brain, body, language and culture, providing an architecture underlying the human capacity for religion. 'Negative' positions develop a non-adaptive stance when they give rise to side-product theories, epiphenomenalism or simply to talking religion down. The vastness of bio-cultural complexity must be the key aspect in any theory of the evolution of religion. Concepts like cognitive niche construction offer new perspectives in gene-culture-coevolution for developing further approaches to the study of religion.

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia
- ▶ Evolutionary Theory in Philosophical Focus

- ▶ Historical Overview of Paleoanthropological Research
- ▶ Modeling the Past: Archaeology
- ▶ Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology

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Paleoanthropology and the Foundation of Ethics: Methodological Remarks on the Problem of Criteriology

Mathias Gutmann and Michael Weingarten

Contents

Abstract

In scientific contexts, human beings are usually categorized as such based on certain stated or implicit membership criteria, i.e., a criteriological framework. Thus, reference to humans as such always raises the seemingly empirical question of which traits should be considered "typically human." Common approaches to this question reveal certain methodological shortcomings. First, the complex grammar of human activities is reduced to an impoverished system of traits, characteristics, and features of biological constitution, and second, the argumentation of criteriological approaches relies on potentially problematic

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M. Gutmann (✉)
Institut für Philosophie, KIT – Karlsruhe Institute of Technology (Universität Karlsruhe TH), Karlsruhe, Germany
e-mail: mathias.gutmann@kit.edu

M. Weingarten
Institut für Philosophie, Universität Stuttgart, Stuttgart, Germany
e-mail: michael.weingarten@philo.uni-stuttgart.de

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animal–human comparisons. A methodologically sound alternative can be provided by developing a more adequate, semantically dense set of concepts in the first step, building on distinctive hallmarks of human existence, namely human work and other activities. From this perspective, the nonhuman-to-human transformation takes place not just within nature (viz. "first nature"), prior to culture (viz. "second nature"); instead it is accepted that we already need to apply our knowledge of human activities in order to explicate "natural transformations" toward a state of being human. Accordingly, nature and culture both constitute inherent aspects of the human life-form itself, and must jointly provide the methodological starting point for the reconstruction of our predecessors. Adoption of this framework has implications for empirical research as well as for ethical judgment: ethical arguments lose their putative foundation in simple physical descriptions of human beings, and paleoanthropology itself has to face up to its often overlooked nondescriptive and normative assumptions.

Introduction

We are used to thinking of entities – irrespective of their nature – as sufficiently characterized by their respective properties, faculties, or capabilities. Thus, hexapods, arachnids, and decapods may be clearly characterized as possessing three, four, or five pairs of legs, respectively. This example illustrates what we might call the epistemological, or "*criteriological*," paradigm: we apply certain criteria, or combinations of criteria, in order to characterize an entity. The limits of this paradigm (which works well in a lot of scientific and, more generally, ontological contexts) become apparent when we refer to something by the *mode of its existence* – as is often the case for living entities. The intuition behind this move away from straightforward physical properties is that living entities "are" in the way they live; to put it with Aristotle, "in living things, to live is to be" (*De anima* II,4,415b13; for discussion see Thompson 2012). The issue is that the predicate "being alive" has a distinctly different structure than, e.g., "being of color x." Particularly when we refer to human beings, we run into problems, well known among philosophers, that arise from the superficial simplicity of certain predicates we use to define humanhood, such as "being social," "having language," or "having culture" – compared with the famous "featherless biped" (with its no less famous counter-example) or the reference to "being anatomically modern." To take the first example, "being social" is not just one characteristic among many of a being called human, but is indeed the very mode of its existence.

Considering the fact that paleoanthropology deals with the reconstruction of life-forms which preceded the human life-form as we know it, one may well wonder whether there are any ethical or even just normative aspects of to the field at all. And indeed, even if any ethical concepts considered relevant to the field were proven to be invalid – whether based on a general decision theory, on a presupposed preference order of values, or on principles of discourse and communicative action – this would not threaten the validity of paleoanthropological statements proper.

When we take a closer look, however, we see that paleoanthropology and ethics share a remarkable premise: both make central reference to human beings as a unique kind of living entity. Even if we were to avoid the identification of "living entities" with "animals," the underlying definitional scheme for human beings would usually be framed in criteriological terms, that is, in terms of membership criteria for certain salient groups. In such definitional scheme, humans can be described as just another kind of animal (however peculiar), with some specific identifying features. In other words, this approach defines humans as "animals plus x," where "x" stands for one or several unique characteristics. The list of such features, whose aim it is to capture the uniqueness of humans, has historically included, e.g., language ability, tool application, sociability, and/or religiousness. Paleoanthropology, then, seems to be in a privileged position insofar as the field provides knowledge on the emergence of those uniquely human characteristics during the prehistoric phase of human evolution. But a closer look at the possibilities of paleoanthropology itself reveals some intriguing methodological problems, which put this privileged status into question:

1. When we attempt to determine the characteristics that define humans, we must refer to a semantic framework which, formally speaking, is significantly denser in the properties it contains than the resulting descriptions. The priority of a semantically dense description would hold even if our descriptions referred to (possibly functionally structured) complex collections of characteristics.
2. Even if we consider paleoanthropology to be our main source of knowledge about what makes a life-form human, the transition from a more or less purely descriptive to a normative argument cannot be justified with reference to this descriptive knowledge alone. This point is of importance when we consider the difference between normative structures that are relevant to scientific descriptions and categorizations, on the one hand, and those of ethical reasoning, on the other.

With respect to the difference between normative structures in science versus ethics brought up in the second point above, it is important to note that we can accept the relevance of several *normative* aspects of descriptions without at the same time accepting their *ethical* relevance. Whereas normativity is assumed to be an inherent aspect of human action, ethical reasoning deals in particular with the (non-inherent) *justification* of human actions. So for example, each speech act will show intrinsic normative aspects that regulate the speaker's and addressee's expectations and (self-)obligations with respect to the utterance. Thus, promising someone to keep a date involves, first, a public self-obligation on the part of the speaker, which in turn results in specific mutual expectations. The violation of this obligation by the speaker, the breaking of the promise, is not necessarily an issue of morality. At least proximately it may be considered to be just some kind of disturbance of the mutuality of expectations that underlie the speech act itself. It is only in a second step, namely when we ask for the *reasons* behind the violation, that we may reach the realm of ethics.

Despite the vast variety of ethical approaches, it is possible to identify certain fundamental argumentative strategies which apply in this arena. Basically, justification of human actions (or of omissions of action) can proceed along one of three different perspectives (following Pfordten 1996):

1. From an *anthropocentric* point of view, the validity of ethical statements necessarily depends on reference to human beings. This necessity can be understood in many ways–depending on the meaning of the term "human." One might take a species-specific approach, or alternatively a discourse-ethical or a utilitarian approach. In all cases the critical fact is that the *authors* of an ethical statement are themselves members of the group of "human beings."
2. Descriptively weaker than anthropocentrism is the *anthroporelational* justification of actions. In this case, only *some* of the steps of the ethical argument must refer to human affairs, whereas elsewhere the justification may integrate nonhuman relationships too.
3. The descriptively weakest approach is *non-anthroporelational* justification. In this case, humans are not at all referred to as the sole or privileged source of moral behavior; nonhuman living entities, and sometimes even nonliving entities, are equally deemed to be bearers of values. These values may be moral, esthetic, or economic. What makes a value relevant within the framework of non-anthroporelational justification is that it is intrinsic, or inherent – a value that exists essentially, without reference to a procedure of evaluation or value ascription. Non-anthroporelational approaches are dominant, e.g., in the field of "eco-ethics" (see the deep-ecology approach of Naess 1989).

In all three types of approaches, the most important methodological problem is the definition of human beings as a (more or less relevant) reference group for ethical ascriptions or descriptions. From a methodological point of view, even an explicitly non-anthroporelational approach has to defend its normative rules, which are supposed to be arrived at by reference to pieces of nature (e.g., "ecosystems"). At least at this point a substantial reference to the process of giving and accepting reasons is unavoidable, which implies that anthroporelational and non-anthroporelational approaches are not as weak (in terms of the validity they claim for normative statements) as they may initially seem to be (for discussion of explicit reasoning see Brandom 1994; for criticism of "nature-centric" approaches see Gutmann and Janich 2002a, b).

Ethics and the Pitfalls of Criteriology

A second taxonomy of ethical approaches is possible that is quite oblique to our first one. Whereas above we dealt with the possible authors and the possible subjects of ascriptions, we will now deal with the procedures that are adopted to reach ethical justification of human actions or omissions. From this perspective, again, a great variety of types of ethical reasoning can be identified, which we summarize here in three well-known categories:

1. The results of human actions – their intended as well as their unintended products and consequences – are the domain of *consequentialist and utilitarian reasoning*. This type of justification brings up at least three systematic problems. First, the profit or benefit–described as a function of the respective action – must be identified. To this end, a relevance ranking or a utilitarian calculus along the lines of Bentham's principle ("Act so as to produce the greatest good for the greatest number"; cf. Bentham 1789; for discussion see e.g., Nida-Rümelin 2005) has to be applied. Second, the authors of the benefits and losses have to be identified; this is often done by assuming that only those entities that show any form of interest in a specific good, or which show a minimal degree of consciousness, need to be taken into consideration. Third, the objects of human actions underlying a specific intervention can be very different in structure. They are assumed to be pure resources and sources of (predominantly) human welfare, and they may even be considered as possible subjects of the ascription of specific rights. These ascriptions may be guided by certain criteria, such as the degree of consciousness or possible interests that the respective targets of the ascriptions are supposed to show or be capable of (this point is of the utmost importance for utilitarian environmental ethics, bioethics, and medical ethics; Habermas 1997; Düwell and Steigleder 2003).

   A prominent example relevant to actual utilitarian reasoning is presented by Singer's (1998 p. 184f) discussion of the fundamentals of practical philosophy. Singer points out that science has helped overcome the "isolation" of humans in nature by leveling the division between "them" and "us." Taking into account the minimal differences between the human species and other life-forms, there seems to remain no sound argument for preferring human life: accordingly, Singer holds, the life of an anencephalic human baby, which might be "used" for organ harvesting, is no more valuable than, e.g., the life of a healthy baboon, just by virtue of the baby being a member of *Homo sapiens*. The "new ethics" represented by Singer's argument, if adopted, would force us to give new answers to old questions – due to the fact that our "position in the universe" has been radically altered. The key, according to Singer, lies in the fact that we no longer have any criterion to unambiguously determine the difference between animals and humans, which previously had provided the foundation of a radically different ethical evaluation of human life versus animal life (for further reading see Singer 1998, p. 184ff.). It follows that humans now are viewed as animals among other animals, with commonly shared features such as sensitivity to pain, consciousness, the ability to take an interest in specific aspects of one's environment, etc. Meanwhile, according to Singer, even within the (biological) species *Homo sapiens* not all members are equipped with these features equally. Thus, some members are equipped with the property of consciousness – to varying degree–while others are not. It is these individual differences that are relevant for the ethical evaluation of the resulting achievements that are potentially available to members of the species *Homo sapiens,* as well as to all nonhuman animals in reference to their respective life-form.

2. From a different point of view, some principles are considered necessary against which human actions may be judged. Those principles can be assumed to be represented by specific inborn characteristics of the human genus *Homo*. Again, human beings appear to be a token of a type, if the type *Homo* is understood as a biological unit. According to Höffe (2002, p. 74) "being wise" (*sapientia*) is the defining criterion, which – as a capability – characterizes all members of the group. By definition then, humans are reasonable animals, equipped by membership in the genus *Homo* with the capability of rational reasoning. From this point of view, the term "life" retains its biological reference. But nevertheless, some differences can be found within the realm of biological entities, considering the specific *form* of life which is represented by the respective natural kind. Accordingly, the term "ethos" has different meanings. In the first place, it defines the life-form, which in the case of animals is mirrored by a natural environment that fits that life-form's biological needs (Höffe 2002, p. 28). At the same time, animals are restricted to a specific form of life, which is essentially defined by their biological equipment – in contrast to human beings. Their individual life is to a certain extent pre-determined by biology, but not entirely: in its first meaning, ethos is something that animals and humans have in common; it refers to their specific place in life, the respective environment of the life-forms. Ethos in the second (tradition) and third meaning (ways of thought, habits, and characters) refers to aspects of life that are specific to humans. The moral attitudes that are represented by the customs of human communities, and the individual characteristics of humans which are thought to be instantiations of the respective customs and habits, are unique human features (Höffe 2002, p. 28f).
3. The central principle of *discursive ethical reasoning* – representing a third major line of argument – is a presupposition of full symmetry and reciprocity in participation and access, on the one hand, and of obligation, on the other hand. Following the concept of an ideal discourse, anybody who might be concerned by a decision should be allowed to participate in the discourse itself. At the same time, full reciprocity and symmetry should hold in accepting the results as well as the consequences of the decision. This is so because the instantiation of any discourse which is at least oriented at the rules of an ideal discourse is based on the *ability* of human beings to participate in rational reasoning – an ability that ultimately rests upon fundamental aspects of human language acquisition. If we trace this acquisition back to its evolutionary origins, the scope of ethical reasoning becomes based on the acquisition of some specific human characteristics, which constitute the crucial difference to any nonhuman, animal constitution. According to Gehlen's program of philosophical anthropology, Niquet (2003, p. 103) conceives humans as "discoursive animals." Thus, even the "most human" characteristic, which is expressed in the biological species name, would be based upon the biological constitution of *Homo sapiens*. Empirical disciplines including cognitive sciences, linguistics, and evolutionary epistemology, "being

> cultural by nature," can provide the knowledge needed in order to finally answer the question why humans are capable of acting discoursively. From this point of view it is only a small step to assume that rationality and language acquisition are real *biological* characteristics, which render possible the unique human abilities for discourse and discoursivity. The human ability to act in accordance with reason would thus be an inborn character of the biological species *Homo sapiens*, culture comes to be seen as a *biological* feature of the genus *Homo,* and humans are understood as animals which inhabit a self-generated environment (Gerhardt 2001, p. 47). Gerhardt explains some of the implications of this view that are relevant for a criteriological definition of human beings. The capability to give and take reasons ultimately is a biologically given criterion; it is supposed to have the same ontic status as the capability to walk upright or to use language. And like the latter, the discoursive capacity belongs to the group – not necessary to the individual. The relation between the individual and its group, then, has a type–token structure, and the basic life-form is characterized criteriologically: discoursivity is framed as a biological characteristic. The orientation of ethical reasoning toward specific characteristics that are assumed to be unique to *Homo sapiens* is one of the central features of this kind of approach; it can also be found in many other types of ethical approaches (for a critical reconstruction of anthropological presuppositions of this type see Wagner and Laubichler 2001).

Although our simple taxonomy above is neither complete nor treats the topic exhaustively, we can already recognize one remarkable similarity in what is presented under each point of view: they all refer (at least in the form of a "weak naturalism," see Habermas 1999) to a criteriological description of human individuals. The transformation from nonhuman to human takes place within the realm of nature: we start with a situation where there are no humans, and we arrive at a situation where there are. And this transformation is accompanied by the acquisition of properties that are explicitly and exclusively human. Accordingly, the difference to animals should be definable in terms of "new" evolutionary characters (*autapomorphies*, in a strict sense of the word). This similarity brings us back to our central assumption: in animal–human comparisons, whenever we use simple labels for properties we run the risk of ambiguity if we do not carefully lay out our theoretical frameworks. The terms "language" or "action" or even "cognition" may come with much richer logical grammars in an evaluative, normative, or ethical framework than in a basic biological context. To show this, we have to examine the issue of characters in a particular paradigm, namely that of evolutionary theory.

The Problem of Characters

Dealing with human beings as animals, we are confronted not so much with normative but with methodological problems concerning the concept of "characters" – in the sense of properties, or features – as applied in evolutionary theory. From a systematic point of view, the situation seems to be clear-cut. Taken as a whole, the universe of living entities, both animals and plants, displays an overwhelmingly large number of characters. Accordingly, the most important task of the systematicist may be seen in the identification of those characters that are useful or necessary for the reconstruction of evolutionary pathways. But classifying characters in this way – that is, by their utility for analytic purposes – entails certain well-known methodological pitfalls, which can be summarized as follows (for an extensive discussion see Sober 1988; Gould 2002; Bock 1988; Wagner and Laubichler 2001):

1. In order to discern "useful" from "less useful" characters, we have to refer to a criterion which has to be established beforehand and permits the specification of individual characters. But to the extent that such criterion is founded on evolutionary knowledge, we either face the risk of making a circular argument, or else the possibility that our criterion turns out to be irrelevant to the classification of characters for the purpose of evolutionary reconstruction (see Peters and Gutmann 1971, 1972; Weingarten 1992). The most promising counter-strategy might be a kind of "hermeneutic" approach, which would at least avoid direct circularity, even though it might not be seen as supporting the phylogenetic validity usually expected of evolutionary reconstructions (for further reading see Reif 2004).
2. Evolutionary reconstructions are guided by certain principles and procedures – such as the principle of "parsimony" – and these principles themselves must be justified in terms of *biological* theory. To do so one could either assume that the principles in question represent the very form of evolution itself, or else treat them as mere methodological choices.

   On the first strategy, parsimony – to use that example – is based on an implicit assumption about the process of evolution, namely that the tree that minimizes change is likely to be the best approximation of the actual phylogeny (for further reading see Rieppel 2007). Evolution is not only modeled *as if it were* some process of optimization, but instead is explicitly defined *to be* a process of optimization. This justification of reconstructive procedures will necessarily fail, however, because it does not address the question of how we can possibly know that evolution *indeed* follows parsimony. Attempts to answer that question will run into a circular argument again, or else we have to concede that it is possible to know the structure of evolution without applying the procedure in question.

   The alternative strategy, as mentioned, is to adopt the principle under discussion – such as the principle of parsimony – simply as a methodological choice for practical convenience. In this case, no justification is given, as the biological interpretation of the principle remains unexamined (for further reading see Gutmann and Janich 2002a, b; Sober 1988).
3. In order to sidestep the issue of the biological naturalness of our reconstructive procedures, as opposed to their being just the result of methodological choices, we might decide to rely on the fact that, all else being equal, probability favors

complex events being unique. In the words of Wägele (2000, p. 41f; translation ours): "The most economical explanation for the interpretation of identical features in organisms rests on an assessment of the probability that the shared feature is due to a shared cause. It is more likely that a complex chain of events (the evolution of an organ with complicated structure) took place only once than that this sequence occurred several times by coincidence."

However, the *improbability* of a transformation taking place more than once does not imply its *impossibility*. And, setting aside this truism, any quantitative probability assessment requires reference to explicit empirical knowledge – which once again brings back the problem of circularity, to the extent that this knowledge is about evolution.

4. Finally, we might be tempted to identify the "likelihood" – or some other kind of immanent criterion – of a given tree as an indication of the tree's correctness, or validity. However, considering that the validity of a tree is always relative to a particular data set, the following objection applies: "It is important to distinguish between the probability of getting the observed data, and the probability of the underlying model being correct. Likelihood says nothing about the probability of the model itself" (Page and Holmes 1998, p. 155). In other words, the consistency of a model must not be confused with its "reality content" – a confusion which is the result of a simple category mistake (for further reading see Sober 1988; Page and Holmes 1998).
5. In addition to this variety of "objective" assumptions on the nature of the organismal features that are supposed to be relevant for evolutionary reconstruction, we can identify a more or less *methodological* line of argument, which refers to the principles of feature recognition itself:
   (a) The strongest approach is taken by a naturalistic interpretation of feature recognition, which implies that living entities "consist" of characters which they simply "have." The identification of characters that are used in the process of structuring nature, e.g. in terms of hierarchies, depends on the "innate" skills of the observer himself (Wägele 2000, p. 13). The resulting type of "evolutionary theory of knowledge" is well established and relies, e.g., on the very fact that the innateness of classificatory abilities does not provide us with valid criteria for the correctness of their application (e.g. Vollmer 1987; Oeser 1987; for a methodological refutation see Janich 1987). However, naturalized epistemologies of this kind face a severe problem of "self-application" by answering the question how we know about the innateness of the respective skills themselves. If an answer is given by reference to the correctness of the classification, a circular argument results (for further reading see Janich 2000).
   (b) A weaker approach would avoid the direct naturalization of feature identification by instead assuming that this process is dependent on the theoretical context at hand. That is to say, it is accepted that if the original taxonomic(!) context of feature description is to be transcended – e.g., in order to establish *systematic* relations between the organisms under investigation – then the specific theoretical context must be taken into consideration, as in the case of

genetic or ecological relations. From this point of view, the conclusion of Wagner and Laubichler is plausible:

> The objects and functional characters that are at the center of every biological theory are not just found objects waiting to be collected in nature, rather they are conceptual abstractions determined by the parameters of a specific theoretical interest (. . .). As such, they can only be identified within the context of the object that is ontologically prior to them. Therefore, a precise formulation of these objects of ontological primacy has to be part of every theory as well. (Wagner and Laubichler 2001, p. 145)

Nevertheless, a methodological alternative to this – however weak – ontological solution of the feature recognition problem is possible, by taking into account the homonymy of one and the same descriptive term serving in different theoretical contexts (such as the term "eye" applied to both *Sepia* and *Pan*). On such approach, the necessity of some theory of the organism can be assumed, which allows the introduction of elementary evolutionary concepts such as the blueprint, or "Bauplan," of a living entity (see Gutmann 2002a; Eckhardt 2000). Wagner and Laubichler express this perspective as follows:

> In other words, we assume the ontological primacy of organisms and derive the objects relevant to the theory, i.e., the biological characters, by means of a conceptual decomposition of the organism. We further argue that if we define biological characters as conceptual abstractions, we also need an appropriately defined organism concept within biological theory. (Wagner and Laubichler 2001, p. 144)

The context dependency of character identification leads to the conclusion that the core problem of biological descriptions is the problem of *comparability*. The truism that only organisms should be compared which are *comparable* then becomes the methodologically most demanding presupposition of character identification. By taking into account that theoretical frameworks are not given per se, but in reference to particular subjects of inquiry ("*Erkenntnisinteressen*") and the respective descriptive and explanatory devices, a methodologically sound alternative even to the weaker types of naturalist concepts can be provided (see Gutmann and Janich 1998).

The above overview on the pitfalls of criteriology has put into focus the challenges of any attempt to define humans contrastively, in comparison with animals. In particular, if we wish to assume that the human-like constitution of an organism is a continuation of animal constitution, the question must be addressed how to deal with those human characters for which we cannot find any antecedents in the animal realm. In order to gain a foothold on this, we must turn to the specific scenarios presented to us by extinct predecessors of human-like organization.

From Remnants to Organisms

Even if we try to apply a character-based description in order to compare humans with nonhuman entities, a distinctive aspect of paleontological research that is relevant when we reconstruct the evolutionary pathways of non-extinct species must be borne in mind. The simple fact is that in the context of organismic descriptions (see below), when we deal with extinct life-forms, we deal with the remnants of formerly living entities. This situation increases the difficulties that we pointed out for criteriological approaches generally:

1. The transformation of the organism as a whole has to be expressed in terms of the transformation of individual characters, or character complexes. Consequently, even functional or reproductive relations must be expressed in terms of characters (Collard and Wood 2000; Wood and Collard 1999; Wagner and Laubichler 2001).
2. We need to assume a representational relation between the organism and those characters used for evolutionary reconstruction. This leads either to the supposition that the character states of current organisms represent evolutionarily older character states (e.g., by maintaining the older character states) or to the conclusion that the current organisms themselves represent an ancestral constitution, as "living fossils."

In both cases, some (valid!) knowledge on the line of evolutionary transformation has to be already available for the identification of relevant characters. Tattersall (1997) underlines the simple fact that it may be impossible to express reproductive continuity in terms of character sequences. The tension between the description of human predecessors and the requirements of a population genetic description of reproductive structure seems to be unresolvable, since it results from what is an empirically insufficient situation:

1. Even if all prehuman fossils found to date are taken into account, the empirical basis of variation analysis seems to be rather speculative. Yet without sound variation analysis, species identification is restricted to a kind of typological differentiation.
2. The reproductive patterns of prehuman populations are assessed in terms of character patterns rooted in typological ordering itself.
3. Fossil remains as well as representatives of genetic traits need to be understood as representatives of specific cultural abilities and technological achievements.

This inconvenient situation is not just the result of a (probably unavoidably insufficient) database; it is a reflex of the nature of paleontology as a scientific project. Because characters need to be integrated into a framework within which they may serve as (biologically) meaningful features of organisms, we have to "interpret" fossil remnants in the light of our biological knowledge. This interpretation leads, in the first instance, not to character sets but to functional designs – to body plans or constructions. These constructions do not represent recent organisms, but rather "possibly viable organisms," which may serve as the predecessors of the known living entities that inevitably constitute our conceptual points of reference. Those functional descriptions of remnants which give rise to the development of a functional plan also refer to functional knowledge borrowed from nonbiological sources (for the procedure, see Gould 1970; Rudwick 1998; Gutmann 2002a; Morris 2003). In describing living entities (belonging to non-extinct species) as if they were functional units, we gain the very starting point of our reconstruction of possible predecessors. One should bear in mind that these constructions are structuralizations of living animals. Thus the transformation next described must be considered as a transformation sequence based on, e.g., biomechanical principles. These principles can be borrowed from engineering practice. When we treat animals as if they were functional units (or "constructions"; see Gutmann 2002a), the transformation of these constructions can be described as either a process of optimization or as a process of differentiation of a given construction in adaptation to different working conditions (for the logic of "*as if*-statements" see Kant 1988 and Lewontin 2000). But because animals are only treated *as if* they were functional constructions, certain fundamental differences to the engineering of machines or engines remain (Gutmann 2005):

1. As in the case of optimizing or developing engines, we start the evolutionary reconstruction with the construction of actual existing forms (biologically described here as functional units). But in contrast to engineering procedures, we *look back* to those constructions that can be regarded as predecessors. This procedure of "retro-engineering" can be formally represented as follows (where K_n stands for the multi-step construction process, with E indicating the terminal construction of actually structuralized animals, and RP are the "reconstruction principles"):

$$K_n\left(A^{\mathrm{RP}}_{K_{n-1}}\right) \Rightarrow \ldots \overset{RP}{\Rightarrow} K_4(A_{K_3}/P_{K_5}) \overset{RP}{\Rightarrow} K_3(A_{K_2}/P_{K_4}) \overset{RP}{\Rightarrow} K_2(A_{K_1}/P_{K_3}) \overset{RP}{\Rightarrow} K_1^E(P_{K_3})$$

2. In the course of optimizing and developing engines, it is often useful and sometimes even necessary to actually shut down and render dysfunctional the artifacts while they are being worked on (though in the case of "Wiener machines" there may be exceptions, insofar as we sometimes need them to be at work in order to optimize them). This marks a fundamental difference to evolutionary transformation lines, because in the latter context each and every "intermediate" reconstruct of a transformation line is required to be "fit for work." In engineering terms, the force-, form-, and material-closure of the intermediates of a biological line of transformation must be maintained during the transformation process itself. Taking into account that we are sometimes confronted with multiple lines of transformation leading back to one and the same starting construction, reconstructed by way of different evolutionary predecessors, it may be more appropriate to speak of differentiation *fields* rather than lines, which are represented as follows (where K again denotes steps of construction, E indicates the terminal construction of actually structuralized animals, RP stands for the "reconstruction principles," DF are the fields of differentiation, and TR the lines of transformation):

$$\begin{tikzcd}
 & & K_{2b} & & \\
 & K_{3_a} \arrow[r, Rightarrow, "RP"] & K_{2_a} \arrow[u] \arrow[d] \arrow[r, Rightarrow, "RP"] & K_1^E & \Bigg\}\mathrm{TR}_1 \\
 & & K_{2_c} & & \\
K_4 \arrow[r, Rightarrow, "RP"] & K_{3_b} \arrow[uu] \arrow[d] \arrow[r, Rightarrow, "RP"] & K_{2_d} \arrow[r, Rightarrow, "RP"] & K_1^E & \Big\}\mathrm{TR}_2 \\
 & K_{3_c} \arrow[r, Rightarrow, "RP"] & K_{2_e} \arrow[r, Rightarrow, "RP"] & K_1^E & \Big\}\mathrm{TR}_3 \\
 & \underbrace{\qquad}_{\mathrm{DF}_3} & \underbrace{\qquad}_{\mathrm{DF}_2} & \underbrace{\qquad}_{\mathrm{DF}_1} &
\end{tikzcd}$$

3. Finally, the antecedent constructions of a given construction are to be "re-interpreted" as the functional "conditions of possibility" of (formerly) living entities (in terms of organismic descriptions). This procedure – which resembles some kind of hermeneutics more than strict scientific deduction – leads to the "envisioning" of possibly viable entities on the basis of the constructional description within a transformation line. This procedure of "reverse engineering" may be represented as follows (abbreviations as above; *Lw* stands for "reinterpretated" animals, for the respective constructions):

$$\begin{tikzcd}
\mathrm{Lw}^{K_n} & \dots & \mathrm{Lw}^{K_4} & \mathrm{Lw}^{K_3} & \mathrm{Lw}^{K_2} & \\
K_n(A_{K_{n-1}}) \arrow[u, Rightarrow] \arrow[r, Rightarrow, "RP"] & \dots \arrow[u, Rightarrow] & K_4\left(A_{K_3}/P_{K_5}\right) \arrow[u, Rightarrow] & K_3\left(A_{K_2}/P_{K_4}\right) \arrow[u, Rightarrow] \arrow[r, Rightarrow, "RP"] & K_2\left(A_{K_1}/P_{K_3}\right) \arrow[u, Rightarrow] \arrow[r, Rightarrow, "RP"] & K_1^E\left(P_{K_3}\right)
\end{tikzcd}$$

For purposes of reconstruction, each construction has to be regarded as a single, coherent functional unit. Consequently, we cannot reduce the reconstruction procedure to the transformation of some individual features or characters. To the contrary: only after the reconstruction is done can we identify the features that may serve as "characters" of evolutionary transformation. The methodology of an "evolutionary hermeneutics" (see Reif 2004; Gutmann 2002a) urges us to anticipate a comprehensive description of those organisms that serve as a source of knowledge on the functional constraints that we are confronted with when dealing with fossil or geological descriptions of ecological settings within which an extinct lifeworld has to be placed. By attempting to characterize human origins in terms of key characters which, once in place, serve to explain the transformation from animal to nonanimal constitution, we are confronted with the same methodological problems explicated above.

Human Characters, Characterizing Humans

When we treat humans as objects of anthropology and replace the term human by "*Homo* sp.," the grammatical structure of our designation implies that humans are animals of a certain kind. Following a common strategy of biological research, we identify the characteristics of those animals that are supposed to be human. By conceptualizing humans as animals we expect to locate their origin within the field of animal organization. We should thus be able to apply the tools which we frequently use to identify the origins of nonhumans. From a methodological point of view, anthropology then becomes a general ontology of being human. Because of human beings' ontological markedness – their exceptional status (in German "*Sonderstellung*"; see Scheler 1947; Plessner 1975) – within the realm of living entities, anthropology is usually accompanied by cosmological considerations. As the philosopher Ernst Cassirer observes, "in the first mythological explanations of the universe, we always find a primitive anthropology side by side with a primitive cosmology. The question of the origin of the world is inextricably interwoven with the question of the origin of man" (Cassirer 1972, p. 3). Both discourses, the anthropological and the cosmological alike, aim at the same question, namely, the problem of *origin*. Human nature is rooted within nature itself, i.e., among the variety of other, nonhuman beings or entities. It furnishes the genus *Homo* with specific and unique properties, abilities, etc. The embedding of human nature into nature as a whole is reflected by the underlying "substance ontology," because it provides the general framework within which all the different entities, constituted as substances, will find their respective places. Relevant aspects of human constitution are usually expressed in terms of defining characteristics such as "l'homme machine, Homo faber, Homo pecans et redivivus, Homo sapiens, Homo mechanicus, Homo sensitivus, Homo negans et patiens, Homo patheticus et divinans, Homo curans, Homo vitalis, Homo oeconomicus, Homo politicus, Homo libidinosus, super-Homo, Homo geometricus" (Scheler 1988, p. 22f; for some methodological criticism of the proposition that humans are cultural entities "by nature," see Weingarten 2001; for further reading see Gutmann 2002b, 2004).

According to this argument, we start with a comparison between animals and humans. A comparison constitutes a three-termed relation between the two things that are being compared and a reference criterion. In order to compare humans with animals, we thus need first to determine the criterion (or criteria) of identity: for example, that (some) animals and humans share, e.g., the same metabolism, or that the DNA sequences of humans may be (more or less) identical with those of (some) animals. However, if these criteria are met we do not then consider humans to be *identical* with animals, but merely deal with them as we deal with animals *in certain respects*. From this point of view we may succeed with the characterization of humans as animals by applying one of two alternative strategies, which we call the homology versus analogy approaches. On the first of these, human characteristics are directly derived from their precursors, and even supposedly defining human properties, such as culture, are understood to have counterparts among animals – a case of homology. Whereas on the second approach, when we assume human characteristics and features as being *like* those of animals, we are dealing with analogy.

Both strategies can be exemplified by empirical studies. We will restrict ourselves here to their respective methodological consequences. When homology is the concept applied, humans are just another type of organisms and, as such, character-bearing systems. Comparing organisms with each other allows us to trace the history of human-specific characters:

> Thus, scientific inquiry based on a homological line of reasoning always has ready justifications. Reconstructions of our phylogenetic past serve the understanding of our morphological design, as well as psychological and behavioral dispositions. Comparative analysis elucidates which features we share with other species and which combinations of traits are different, in particular with respect to ecologically similar species. Information like this can illuminate biological foundations (i.e., constraints and conditions, of human culture). (Weingart et al. 1997, p. 151)

Following this line of thinking, human nature becomes fundamental for culture: the capability to generate culture precedes the actualization of culture, and observed culture becomes a more or less direct expression of human nature's (biological) structures. Accordingly, the ability to create culture is conceptualized in terms of characters again, as we saw above, and thus must – by definition – be acquired due to evolutionary transformation. The same methods are applied as in the reconstruction of evolutionary transformation with respect to more "standard" characters (see section "The Problem of Characters"); culture is to be understood as the result of transformations of characters that constitute human nature itself. Culture then becomes the extended focus of evolutionary theory (with different cultures as tokens of a type expressing the capability for developing culture) and we have to consider the guiding difference between nature and culture as a result of natural transformation processes. In consequence we are urged to search for culture-invariant features which are shared by virtually all members of the species *Homo sapiens,* understood now in terms of natural kinds (for some problems concerning the "correct" determination of the genus, see e.g., Tattersall 1997 or Wolpoff and Caspari 1997; for further discussion see Griffiths 1997). Additionally, culture becomes a kind of evolutionary force or mechanism of a very peculiar kind (for a radical approach of this type see Dawkins 2009).

The inherent problems of such an attempt become apparent when we try to determine, for example, the fitness value of one of Beethoven's symphonies. Setting aside, for the sake of the argument, the empirical problems that accompany the homology approach (discussed by Lewontin 1961; Lewontin et al. 1984; Gould 1988), a wide array of methodological problems remains to be solved. The methodological shortcomings are closely linked to a confusion of different levels of descriptions: The *explanandum* of a homology approach is determined at the language level, without relevant biological implications. Thus we may in fact describe, e.g., the harmonic and structural development of a classical symphony without referring to any biological or evolutionary implications. With reference to evolutionary theory or population genetics, terms like "music" tend to be meaningless.

Alternatively, we might explicitly attempt to explain the *biological* role of music in terms of biological theory. In this case, not the music itself but rather its biological role provides the *explanandum*. However, in taking this track we reproduce the methodological shortcoming of our previous explanatory attempt (see, e.g., Eibl-Eibesfeldt 1997), as we now need to derive music from its biologically described forerunners, which implies the need to determine the fitness value of music per se. The dependence of the *explanandum* on our choice of description will probably undermine our biological analysis right from the start, because there are no biological criteria for, e.g., membership of a given composition in the canon of classical compository art.

A weaker assumption is provided by variants of the analogy approach, which stand in a certain contrast to the homology approach. On the analogy approach, humans are not understood *as* animals but *like* animals. As explicated in Gutmann et al. (2010), analogy approaches claim that the cultural unfolding of humans resembles, in certain limited aspects, the evolutionary process deemed to govern the development of animals. Due to this decisive methodological difference, the central problem of the homology approach is avoided: we do not have to claim that identical *mechanisms* are at work in cultural development, on the one hand, and evolutionary transformation, on the other. In the words of Weingart et al. (1997):

> The basic differences between changing cultures and changing biological populations preclude mere subsumption. It is commonly understood that new cultural practices can be produced in direct response to perceived needs, unlike the randomly generated novelty in evolutionary processes. It is sometimes supposed that this process makes sociocultural theories in terms of the Darwinian model impossible. (Weingart et al. 1997, p. 286)

However, this obvious advance – compared with the shortcomings of homology approaches – comes at a price: to the extent that cultural development can be understood as the result of unique and biologically irreducible processes, the original dualism between nature and culture re-emerges. The most radical exposition of this dualism is presented by Cassirer, who holds that there are indeed unbridgeable differences between nature, on the one hand – which follows a "Darwinian mode" of inheritance – and culture, on the other hand – which follows a "Lamarckian mode" of transformation (Cassirer 1993, p. 126). The key claim here that this difference is not a natural one – that is, not the kind that might be bridged by some version of a "cultural evolution" approach (see Chapter 17yy). It is a methodological difference, originating in two irreducible language games juxtaposed by "analogy" (e.g.: "Tradition is something like evolution"). The resulting "analogy" between the two processes is expressed in terms of a metaphorical description of some central aspects of the human world itself, i.e. without reference to presumed underlying biological concepts. Cassirer's use of a "metaphorical" description of culture – as if it were nature – provides the relevant clues for the solution of the underlying methodological problem (we will pursue these clues in the next section, where we will present a methodologically sound alternative).

The methodological problem consists in the indeterminacy of the concept of analogy, which is assumed to (non-reductively) connect culture to nature. From a formal point of view, an analogy has the structure of a comparison. Let A and B be two entities of different kinds, and let them both have property P. If we additionally know that A displays property Q, we may infer “per analogiam” that B displays the same property. The inference is adequate, however, if Q is implied by P; thus, the syllogism of analogy is either incomplete or non-conclusive. And if it is complete, it becomes just what an analogy was not supposed to be, namely an inference proper. (A good example for analogical reasoning, however misguided, is provided by the s.c. physico-theological proof for the existence of good; for further reading see Gutmann and Warnecke 2006.)

However, despite the indeterminacy problem, “analogies” are often applied as heuristic procedures, in order to structuralize an object in the light of some knowledge – or operational know-how – which was originally gained in a different field of research. Take for example the comparison of a neuron with a piece of electric circuitry, a comparison which leads to the image of an electric grid that is supposed to represent certain electric properties of signal transfer along an axon (s. Hodgkin and Huxley 1952). In this case, we may use the laws of electricity in order to structuralize *biotic* units (neurons) “as if they were” electrical units – that is, artifacts. In doing so we are not stating that neurons *are* artifacts or electric units, but only that some of the *biological* functions of the *biotic* units can be modeled in terms of electric circuitry. However, the explication of the metaphorical phrase “The neuron is some kind of electric circuitry” (which it very obviously is not) allows us to construct some experimental systems that finally lead to a useful *model* based on our approaching neurons as if they were an inanimate object of the relevant kind. The metaphor itself is lost (to a certain extent) and supplanted by the model (for further reading see Gutmann et al. 2010).

The limitation of an analogy then is of a methodological nature, as it remains in the logical grammar of “as if”-relations. This corresponds to the use of the term analogy in contexts where humans are considered to be like animals. If culture is the explanandum, which is to be explained on grounds of analogy, then the explanation will work only if we describe the process of cultural development in terms of reproductive relations. In this case the transformation of species becomes the explanans – *per analogiam* – for the development of culture(s), which might finally lead us to some “phylogeny of culture” (Boyd et al. 1997, p. 364). In order to explore the analogy, it is necessary to cast it in the terminology of species evolution, with reference to properties like “sexually reproducing,” “mutually reproductively isolated,” “highly integrated,” “genetically programmed,” or whatever characters we wished to use (see, e.g., Mayr 1997). But since we are only dealing with phylogeny in these explorations of “as if,” the explanatory power of the analogy remains within the general limits of “as if”-statements – unless we were willing to assume that humans are not just *like* animals but that they literally *are* animals. In the latter case, the analogy argument becomes indistinguishable from the homology approach and the presumed advance concerning the strength of the premises and implications is lost, giving way to the very familiar picture of a classic reductionist line of thinking (for further reading see Gutmann 2004, 2014).

Irrespective of differences in detail, both approaches lead to the same unsatisfactory conclusion, namely, that the treatment of culture on the basis of a character-oriented approach arises from a category mistake, indicated here by the confusion between two different language games. However, as we will now show, we may gain an alternative by defining culture not in terms of characters but as an expression of human activity.

Nature-Culture and Culture-Nature as Aspects of Human Work

As we saw, humans can be defined in terms of culture, which comprises all the differences we may identify in comparing humans with animals. However, we just demonstrated that culture itself cannot be treated as a character without running into logical and methodological difficulties. Mediation-oriented approaches provide an alternative, as both aspects – nature and culture – are there interpreted as the constituents of a relation, not as independently defined concepts. Cassirer's functionalist approach of symbolic forms exemplifies this argument, at least to a certain extent (see Gutmann 2004).

In stark contrast to character-oriented approaches, Cassirer focuses on inter-individual and intersubjective relations that constitute culture, as well as on the relations between culture(s) and (their respective) nature(s). For instance, he has this to say about 'truth':

> Truth is by nature the offspring of dialectic thought. It cannot be gained, therefore, except through a constant cooperation of the subjects in mutual interrogation and reply. It is not therefore like an empirical object; it must be understood as the outgrowth of a social act. Here we have the new, indirect answer to the question "What is man?" Man is declared to be that creature who is constantly in search of himself–a creature who in every moment of his existence must examine and scrutinize the conditions of his existence. In this scrutiny, in this critical attitude toward human life, consists the real value of human life. "A life which is unexamined", says Sokrates in his Apology, "is not worth living." (Cassirer 1972, p. 5f)

The "life worth living" here is understood as the expression of an ongoing process of self-reflection and self-constitution – a process which shapes the specifically human type of world-reference, being derived from the structure of mediated self-reference. The means, media, and patterns *by*, *through,* and *according to which* this mediation takes place, then, are the actual subject matter of reflection; they provide the "symbolic forms" that give shape to human–world relations. These symbolic forms – such as language, myth, art, knowledge – constitute, enable, and structure all human activities; and furthermore, they are the forces of development for these activities themselves. The transformation of human beings is not the result of random external forces but of the transformation of human beings' activities – forced and fuelled by the transformation of their respective (symbolic) forms. Due to the way this immanent process takes place, "external" relations are transformed together with their respective referent. Hence "nature" is not just "non-culture," but a reflection of the transformative effects of human activities, i.e. a reflection of human work. Again in Cassirer's words: "Man's outstanding characteristic, his distinguishing mark, is not his metaphysical or physical nature but his work. It is his work, it is the system of human activities, which defines and determines the circle of "humanity". Language, myth, religion, art, science, history are the constituents, the various sectors of this circle" (Cassirer 1972, p. 68).

Work is understood, on this view, as collective activity mediated by tools, which permanently generates and reproduces the difference between nature and culture. Reproduction in this sense does not refer to genetic reproduction but to the development and transformation of tools and the conditions of their use, *as part of their being used*. And it is work that provides us with the very starting point for "symbolic reconstruction" – that is, a reconstruction of mediated human activities which are not just the result of the organic activities of some specific life-form (namely humans, defined as members of *Homo sapiens*), but rather the result of the entire symbol systems, which gave these activities their respective form. Thus, the relations between the producers and the products, between the aims and purposes identified, the means and tools applied, and finally the relations between the individuals themselves using symbols – and transforming them by using them – are all to be taken into consideration. A markedly comprehensive definition of "humanity" will result from unfolding and exploring the immanent structure of these symbolic forms as well as their ongoing transformation. We are gaining a "generic" definition of "being a human being" *qua* "being human" (cf. Gutmann 2011 on the notion of "human life").

Based on a comprehensive conception of "human being" of this kind, even criteriological characterizations become conceivable, if they refer to conditions that are necessary in order not only to produce but to reproduce symbolic relations:

> Language, art, myth, religion are no isolated, random creations. They are held together by a common bond. But this bond is not a vinculum substantiale, as it was conceived and described in scholastic thought; it is rather a vinculum functionale. It is the basic function of speech, of myth, of art, of religion that we must seek far behind their innumerable shapes and utterances, and that in the last analysis we must attempt to trace back to a common origin. (Cassirer 1972, p. 68)

Setting aside the shortcomings of Cassirer's own concept of this origin (which ultimately leads to some Uexküllian-style functional circuit), the reference to human activities as the expression of the human life-form provides us with a non-reductivist understanding of "being human." The resulting double-barrelled process of analyzing the structure of mediated human activities and tracing back their origins represents a central issue in mediation-oriented approaches (see Gutmann 2004). We are now prepared to use the insights gained within such an approach toward a reconstructive understanding of human beings even in the context of paleoanthropological descriptions (for further reading see Gutmann et al. 2010).

Defining Humans by Their Activities: The Problem of the Methodological Starting Point

Reconstructions of the kind presented above are adequate tools for historical explanation. Such explanations presuppose a semantically rich description as a methodological starting point. The richness of this starting point (applied to human beings) contrasts with the thin semantics of scientific descriptions (applied to organisms generally) because the logical grammar of the human world differs fundamentally from the grammar of its physical or biological descriptions. Based upon the differentiation between the resulting two distinct modes of discourse, namely that of ordinary experience, on the one hand, and that of empirical sciences, on the other, Kambartel (1989) identified a fallacy of category. This fallacy comes into play when we assume a scientific foundation, or "substruction" (Husserl 1963), underlying ordinary experience itself. This substruction ultimately results in the assumption that ordinary language and experience is nothing else than a special case of scientific experiences, characterized by a relative lack of exactness and acuteness (see Gutmann and Rathgeber 2011). The semantic richness and thickness of ordinary language then would appear to be a sign of a conceptual shortcoming rather than an advantage. However, in offering scientific explanations – irrespective of their specifics – we are still explaining *something* in reference to some explicit knowledge, which latter constitutes the *explanans* in the explanatory schema. It is this necessary reference to *something* that is being explained which generates the categorical difficulties, because this *explanandum* (the "something" we are aiming at by applying our explanatory schema) has to be *described*. And it is the adequacy and validity of this description that has to be determinable without direct reference to the *explanans*. Consequently, the direct transition from a scientific context, e.g., a physically or chemically described situation, to a situation of perception or moral judgment – taking place in terms of ordinary experience, dealing with persons and interpersonal relations – is *grammatically* (not empirically) excluded (Kambartel 1989, p. 67). Accordingly, evolutionary reconstructions should be – methodologically – considered as *narratives* that refer a grammatically thinner description (the *explanans*) to a grammatically richer situation (the *explanandum*). The resulting shift from one language of description to another (each with its respective unique grammar) should not be confused with the transition from one state of nature to a second, more complex state of nature. Consequently, the narrative itself becomes methodologically indispensible: according to Kambartel (1989, p. 67) it is only through the creation of a historical narrative that we can relate to the origins of the new grammatical situation.

This grammatical differentiation permits a powerful rejection of reductionist scientific approaches, not only within the confines of evolutionary biology. Moreover, it provides a solution for our problem of scientifically dealing with humans as specimens of *H. sapiens* without reducing them to this description (for the model-theoretical background, see sections "From Remnants to Organisms" and "Human Characters, Characterizing Humans"). In order to do so, we must remind ourselves that we are facing a multitude of different language games and their respective language worlds. The gap between the human world (seen from the perspective of everyday life-world experience) and the world of animals (including humans), plants, physical and chemical objects (in terms of scientific descriptions) can be bridged by means of narrative explanations. Not surprisingly, the complexity of the descriptive language, and the "thickness" of the resulting description, will to some extent resemble the complexity of the described object itself. It makes sense, in light of this fact, that in recent paleoanthropological approaches we are increasingly often confronted with “scenario” techniques (for some methodological reconstructions see Gutmann et al. 2010). The main difference to “classic” approaches, the form of which we explicated above, consists in the – sometimes extreme – complexity of the *explanans*. However, even in the case of scenarios, the fundamental requirement regarding the validity of scientific statements (here, paleoanthropological reconstructions) remains the same as in the more simple case of reconstructive transformation sequences: the connection between the human world and nature must be drawn through narratives. Some intriguing dualisms results from this differentiation between nature and culture; inhabiting the world of persons, having intentions, giving and accepting reasons for one’s own and others’ actions, etc., become irreconcilably separated from the world which the scientific statements themselves refer to. Wilfrid Sellars put it thus:

> To think of a featherless biped as a person is to think of it as a being with which one is bound up in a network of rights and duties. From this point of view, the irreducibility of the personal is the irreducibility of the ‘ought’ to the ‘is’. But even more basic than this (. . .) is the fact that to think of a featherless biped as a person is to construe its behaviour in terms of actual or potential membership in an embracing group each member of which thinks of itself as a member of the group. Let us call such a group a ‘community’. (Sellars 1963, p. 39)

Following Sellars’ argument, a bridging of the gap between science and the everyday life-world seems to be possible, at least to a certain extent, through integration of the scientific image of man into the “manifest” image of ordinary (non-scientific) experience. In Sellar’s words:

> Thus the conceptual framework of person is not something that needs to be reconciled with the scientific image, but rather something to be joined to it. Thus, to complete the scientific image we need to enrich it not with more ways of saying what is the case, but with the language of community and individual intentions, so that by construing the actions we intend to do and the circumstances in which we intend to do them in scientific terms, we directly relate the world as conceived by scientific theory to our purposes, and make it our world and no longer an alien appendage to the world in which we do our living. (Sellars 1963, p. 40)

An alternative strategy, however, would be to cast the sciences themselves as a constitutive part of the human life-form, rendering the scientific perspective a very specific instance of the standardization of perspectives which are provided by ordinary life (e.g. Heidegger 1993; for further reading see Gutmann 2011).

Conclusion I: The Shortcoming of Criteriology in Paleoanthropology

We can avoid a dualism of this kind if we take into account Cassirer’s definition of human beings by referring to their respective mediated activities. This most comprehensive definition provides us with our methodological point of departure. Referring to human activities, we can even provide sound biological descriptions of aspects of these activities. Starting with physical activities, such as the specific human mode of upright walking, the specifics of human phonation and speech, etc., we are able to elaborate scientific descriptions that serve as the methodological points of departure for the reconstruction of possible antecedent human constitutions. As we pointed out before, the resulting reconstructions in terms of “possibly viable organisms” (in the sense of pre-human life-forms) take into account that we need the reference to further language games (and their underlying practices) for life-scientific purposes, namely all the discourse conventions of non-biological, technical, physical, and chemical knowledge and know-how that we used in order to achieve our functional descriptions of living entities (in the *as if*-mode). Accordingly, we can identify three asymmetries, which are often confounded when we do not distinguish between reference to humans *insofar as they are human* and to humans *as biological objects* (organisms):

1. Biological (genetic, physiological, morphological, etc.) descriptions of human beings (as if they were merely living entities) depend necessarily on non-biological knowledge and know-how; in contrast, physics or chemistry can exist without reference to biology.
2. Among other scientific points of reference, paleoanthropology refers to *biological* knowledge (particularly in terms of functional descriptions) of recent life-forms. However, functional biological knowledge can have validity without further reference to paleoanthropology.
3. Scientific descriptions of human beings refer necessarily to (self-)descriptions of human beings *as being human* (images of man-in-the-world, in Sellars’ terms). Their validity and adequacy can be claimed only in the context of non- and prescientific practice and communication. Sciences then are considered to be embedded into human culture–as a (specific and highly relevant) aspect of this culture.

In light of these observations, we can give deeper reasons for the shortcomings of a criteriological foundation of paleoanthropology. When we deal with (nonhuman) living entities as *biological* objects, we describe them in the light of our self-knowledge, thereby applying our technical and scientific knowledge and know-how in terms of organismic descriptions and structuralization. In the specific explanatory framework we have used here, they are described “as if they were” functional units. The relation between the authors (e.g., scientists) and the objects (nonhuman living entities) of description changes fundamentally when the authors themselves become the object of their description, because in the process they refer to themselves as a kind of object that differs from other objects by some specific criteria. In the field of concern to us here, biological or paleoanthropological descriptions of human beings need to be considered as descriptions of humans “as if they were just organisms” – such as animals (viewed as a type of organism). As the philosopher Edmund Husserl, born in 1859, observed on this double-barreled procedure of constitution (of norms, guiding the structuralization), on the one hand, and actual objectivation (via ascription and modeling) of human beings “as animals”, on the other:

> Among the problems of abnormality the problem of nonhuman animality and that of the levels of, higher and lower 'brutes are included. Relative to the brute' man is, constitutionally speaking, the normal case – just as I myself am the primal norm constitutionally for all other men. Brutes are essentially constituted for me as 'abnormal' variants of my humanness, even though *among* them in turn normality and abnormality may be differentiated. (Husserl 1960 (1931), p. 126)

If we overlook the inversion of the "as if"-relation, a (possible and possibly valid) criteriological description gains the methodological status of a statement on the essence of the human constitution. This indispensable asymmetry between a (thinner) scientific description and its (thicker) methodical starting point has implications that are most relevant as the preconditions of a scientific (here: paleoanthropological) foundation of ethics.

Conclusion II: The Criteriological Failure of Ethics

In criticizing criteriological approaches in ethics, we have reached a seemingly curious situation. On the one hand, the pitfalls of ethics can be recognized when we take into consideration the methodological problem, with which paleoanthropological research is confronted. Here, we identified the necessity of starting with a semantically very rich description of human beings, their activities, and the very form of those activities, if only to gain a methodological starting point for a semantically thinner description of humans as biological entities – named *Homo sapiens*. This, however, leads to the difficulties we identified of characterizing the transformation of a nonhuman into a human constitution as a transformation from nature to culture which remains nevertheless embedded into nature. Thus, the anticipation of the semantics of humanity is obscured by its translation into a biological language of characters. On the other hand – and this is the second part of the aforementioned curious situation – the *normative* deficiency of paleoanthropology becomes observable by explicating the semantics of a description of humans *as being human* and their activities in order to provide some basis for ethical reasoning itself. Even by articulating a simple description of human beings as members of *Homo sapiens*, we claim at least its adequacy – and this claim cannot be replaced by an alternative description. So, even if we considered scientific theories to represent states of the world, at least the evaluation of the adequacy of these representations cannot be given in a purely descriptive language again. This dilemma has its very origin in the structure of criteriological characterizations of human beings, in both the field of paleoanthropology as well as that of ethical reasoning.

Cross-References

- ▶ Charles Darwin, Paleoanthropology, and the Modern Synthesis
- ▶ Cultural Evolution During the Middle and Late Pleistocene in Africa and Eurasia

- ▶ Evolutionary Theory in Philosophical Focus
- ▶ Evolution of Religion
- ▶ Historical Overview of Paleoanthropological Research
- ▶ Homology: A Philosophical and Biological Perspective
- ▶ Modeling the Past: Archaeology
- ▶ Principles of Taxonomy and Classification: Current Procedures for Naming and Classifying Organisms
- ▶ Species Concepts and Speciation: Facts and Fantasies
- ▶ The Evolution of Speech and Language
- ▶ Theory of Mind: A Primatological Perspective

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Subject Index

This index includes suprageneric taxa.

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Taxonomic Index

This index contains only genera and species.